REFERENCE: Varela SAM, Matos M & Schlupp I. 2018. The role of mate-choice copying in speciation and hybridization. Biological Reviews 93(2): 1304-1322. doi: 10.1111/brv.12397.

This is the accepted version of the manuscript

The role of mate-choice copying in speciation and hybridization

Susana A. M. Varela[1]*[§], Margarida Matos[1] and Ingo Schlupp[2]

[1]cE3c – Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal.

[2]Department of Biology, University of Oklahoma, 730 Van Vleet Oval, Norman, OK 73019, USA.

***Address for correspondence** (Tel: +351 21 7500000 ext. 22350; E-mail: savarela@fc.ul.pt).

[§]**Present address** (Instituto Gulbenkian de Ciência, Oeiras, Portugal).

Word count: 16501

ABSTRACT

Mate-choice copying, a non-genetic mechanism of mate choice, occurs when an individual (typically a female) copies the mate choice of other individuals via a process of social learning. Over the past 20 years, MCC has consistently been shown to affect mate choice in several species, by modifying genetically-based mating preferences. This behaviour has been claimed by several authors to have a significant role in evolution. Because it can cause or increase skews in male mating success, it seems to have the potential to induce a rapid change of the directionality and rate of sexual selection, possibly leading to divergent evolution and speciation. Theoretical work has, however, been challenging this view, showing that copying may decelerate sexual selection and that linkage disequilibrium cannot be established between the copied preference and the male trait, because females copy from unrelated individuals in the population, making an invasion of new and potentially fitter male traits difficult. Given this controversy, it is timely to ask about the real impact of mate-choice copying on speciation. We propose that a solution to this impasse may be the existence of some degree of habitat selection, which would create spatial structure, causing scenarios of micro-allopatry, overcoming the problem of the lack of linkage disequilibrium. As far as we are aware, the potential role of mate choice copying on fostering speciation in micro-allopatry has not been tackled. Also important is that the role of mate-choice copying has generally been discussed as being a barrier to gene flow. However, as we see it, mate-choice copying may actually play a key role in facilitating gene flow, thereby fostering hybridization. Yet, the role of mate-choice copying on hybridization has so far been overlooked, although the conditions under which it might occur are much more likely, or less stringent, than those favouring speciation. Hence, a conceptual framework is needed to identify the exact mechanisms and the conditions under which speciation or hybridization

are expected. Here, we develop such a framework to be used as a roadmap to future research at the intersection of these research areas.

Key words: Sexual selection, social learning, mate-choice copying, sexual imprinting, speciation, hybridization, extinction risk, species recognition, reproductive interference.

CONTENTS:

VII. References

I. INTRODUCTION

Ever since Darwin's theory of sexual selection (1859; 1871), a key question in evolutionary biology is how sexual organisms, mostly females, choose their mates. If being choosy is more beneficial than random mating, females need information about male variability in quality in order to make optimal and adaptive decisions. The question is, therefore, what information do females use before accepting or rejecting a mating invitation?

The classic view has been that females have innate, or genetic, preferences for certain male phenotypes, which remain fixed throughout their lives. Genetically inherited information is the product of selection and reflects long-term adaptations to past environments. Those adaptations are important because they tend to associate species with particular kinds of habitat and social contexts, where they develop unique life-histories and social skills that distinguish species from one another. Female genetic preferences for males with particular traits are thus considered adaptive evolutionary responses to genetic and phenotypic indicators of the benefits that a male can provide to the female as a mate. Different genetic mechanisms of female mate choice evolution include direct benefits, sensory biases, Fisherian sexy sons, genetic benefits, and genetic compatibility (Andersson, 1994). Though the relative importance of each mechanism may not be easy to demonstrate in all cases (Andersson & Simmons, 2006), the genetic theory of sexual selection has been widely supported (Fisher, 1930; Kirkpatrick, 1982; Majerus, 1986; Andersson, 1994; Mead & Arnold, 2004; Andersson & Simmons, 2006). Moreover, female choice is known to have an impact on speciation (Lande, 1981; Coyne & Orr, 2004; Kraaijeveld, Kraaijeveld-Smit & Maan, 2011; Nosil, 2012).

Nonetheless, researchers are increasingly aware that females may not exclusively select mates based on their innate preferences. Indeed, the quality of sexual partners is

not constant within a population, since it may vary with the ecological context and with the males' ontogeny, namely their phenotypic condition and age (Stearns, 1992; Kokko, 1997; Danchin *et al.*, 2004; Danchin, Giraldeau & Wagner 2008; Harrison *et al.*, 2013). Hence, genetically inherited preferences by females may not always adequately reflect male quality. As a complement, mate choice decisions may also be influenced by a female's social environment and learning processes. Such social learning processes can lead to shifts in female innate preferences, that can cause or increase skews in male mating success, affecting the directionality and rate of sexual selection (Wade & Pruett-Jones, 1990; Laland, 1994a; ten Cate, 2000; Verzijden *et al.*, 2012; Santos, Matos & Varela 2014).

Because of that, several researchers have suggested that non-genetically inherited information, particularly in the context of sexual selection, can affect speciation (e.g., Laland, 1994a; Jablonka, Lamb & Avital, 1998; ten Cate, 2000; Danchin *et al.*, 2004; Danchin & Wagner, 2008; Grant & Grant, 2009; Danchin & Wagner, 2010; Danchin *et al.*, 2011; Verzijden *et al.*, 2012; Dukas, 2013; Laland *et al.*, 2015; Lindholm, 2015). «Ecological feedbacks, speciation, and evolutionary dynamics not only result from gene flows, but also more generally from 'information flows' among demes» (Danchin, 2013). In other words, developmental processes, like social learning during mate choice, can «create novel variants, contribute to heredity, generate adaptive fit, and thereby direct the course of evolution» (Laland *et al.*, 2015).

Previously, emphasis has been given to the role of sexual imprinting in speciation (Laland, 1994b; Grant & Grant, 1997; Irwin & Price, 1999; Owens, Rowe & Thomas, 1999; ten Cate, 1999; ten Cate, 2000; Verzijden *et al.*, 2012; Lindholm, 2015), as it is a type of preference learning that happens very early in the life of an organism and that has a remarkable stability throughout life, affecting mate choice once the organism reaches

137 sexual maturity (Lorenz, 1935; Immelman, 1975). Maternal imprinting, in particular,
138 generates assortative mating, maintains male polymorphisms and preserves linkage
139 disequilibrium between the female preference and the male trait, which are the necessary
140 ingredients for sympatric speciation (Verzijden, Lachlan & Servedio, 2015; Verzijden *et*
141 *al.*, 2012). But beyond sexual imprinting, mate-choice copying is the best example of a
142 learning process influencing mate choice, with properties of its own (see Table 1).

143 Mate-choice copying occurs much later in life than sexual imprinting, when a
144 sexually mature individual, though potentially inexperienced, observes and copies the
145 mating decisions of other individuals, by a process of social learning (Pruett-Jones, 1992;
146 Dugatkin, 1996a). Over the past 20 years, mate-choice copying has consistently been
147 shown to affect mate choice in a variety of species, by replacing genetically-based mating
148 preferences (see reviews in Vakirtzis, 2011 and Witte, Kniel & Kureck, 2015). The
149 consequences are that the selection pressures on both copying and copied individuals can
150 change radically, affecting the direction and strength of sexual selection. This is why it
151 has been suggested that mate-choice copying may cause speciation if its effects persist
152 long enough in the behaviour of copier individuals (e.g. Gibson & Höglund, 1992;
153 Brooks, 1998; Witte & Noltemeier, 2002; Danchin *et al.*, 2004; Danchin & Wagner, 2008;
154 Mery *et al.*, 2009; Leadbeater, 2009; Fowler-Finn *et al.*, 2015) (Table 1).

155 What is poorly understood, however, are the exact conditions, and their
156 likelihood, under which mate-choice copying can effectively cause speciation. In contrast
157 with the impact of maternal sexual imprinting, speciation by mate-choice copying needs
158 to occur under more stringent conditions, because it tends to generate positive frequency
159 dependence for the most common male phenotype, which makes it difficult to maintain
160 polymorphisms, and because linkage disequilibrium cannot be established between the
161 copied preference by the female and the male trait (Verzijden *et al.*, 2005; Verzijden *et*

al., 2012). Fine-grained habitat structuring (micro-allopatry), with some degree of ecological barriers (particularly involving habitat selection), seems necessary for mate-choice copying to be able to create and stabilise behavioural isolation. In the present paper, we thus provide a detailed analysis of the very particular circumstances under which mate-choice copying can disrupt and canalise female mating preferences for certain male phenotypes, creating and potentiating divergence and speciation.

Similarly to sexual imprinting that sometimes may also initiate hybridization events – when animals misimprint on heterospecifics' traits, such as e.g. morphology or vocalizations, making them recognize heterospecifics as quality mating partners (ten Cate & Vos, 1999; Grant & Grant, 1996; Grant & Grant, 1997; Irwin & Price, 1999; ten Cate, 2000) – we additionally propose the hypothesis that mate-choice copying may also favour hybridization, by increasing female acceptance of heterospecific male phenotypes. This can happen when heterospecific demonstrator females are seen as good models to copy (Hill & Ryan, 2006), as well as when conspecific model females mate with heterospecific males (Schlupp, Marler & Ryan, 1994; Heubel *et al.*, 2008). We suggest that – just as in sexual imprinting – copying "mistakes" can be caused by incomplete species' recognition systems and could lead to successful hybridization, but also to reproductive interference. This potential role of mate-choice copying in promoting hybridization has been so far overlooked, though the conditions under which it might occur are much more likely, or less stringent, than those favouring speciation, which could be indicative of its importance. We thus propose for the first time that mate-choice copying may cause hybridization and that it can contribute, if hybridization is successful, to either the establishment and/or maintenance of hybrid zones, or to new reproductive isolation. If, on the other hand, hybridization is unsuccessful, with fitness costs to both the copying and copied individuals, mate-choice copying can lead to reproductive interference,

increasing species extinction risk. As a result, there might be selection against mate-choice copying, or selection to reinforce species recognition, thereby, preserving or reinforcing reproductive barriers. In the following sections, we discuss scenarios and mechanisms by which mate-choice copying can weaken or strengthen gene flow within and between populations, with consequences for both speciation and hybridization.

II. MATE-CHOICE COPYING, A NON-GENETIC MECHANISM OF SEXUAL SELECTION

(1) Mate-choice and reproductive isolation

Sexual selection, along with natural selection and, to a lesser extent, mutation and genetic drift, are mechanisms that can cause reproductive isolation between populations (Coyne & Orr, 2004). In particular, sexual selection through assortative mating creates behavioural isolation, which along with temporal isolation, habitat isolation and immigrant inviability, is a type of prezygotic barrier to gene flow (Coyne & Orr, 2004; Nosil, Vines & Funk, 2005). There is behavioural isolation when individuals from allopatric or sympatric populations do not recognize each other as suitable mates or are less attracted to mate with each other than with individuals of their own populations (Mayr, 1963; Futuyma & Mayer, 1980; Lande, 1981; Coyne & Orr, 2004; Mead & Arnold, 2004; Nosil *et al.*, 2005; Kraaijeveld *et al.*, 2011; Mendelson & Shaw, 2012; Nosil, 2012) (Fig. 1).

The evolution of behavioural isolation between potential partners can either occur primarily at the level of female mating preferences or at the level of male secondary sexual characters (Coyne & Orr, 2004; Verzijden *et al.*, 2012). In both cases, there is co-evolution of male and female traits, respectively, along with sexual conflict, female

212 cryptic choice, and male-male competition (Andersson & Simmons, 2006). Non-genetic
213 mechanisms of sexual selection (social learning) can also affect both female preferences
214 and male sexual traits. Females can learn with whom to mate and males can learn to signal
215 their sexual traits, that is, they can learn how to display (ten Cate, 2000; Verzijden *et al.*,
216 2012; Dukas, 2013). This is the case, for example, in song learning in birds, where
217 females learn to prefer sexual partners with similar display songs to their fathers and
218 males learn from their fathers how to sing those specific songs (ten Cate & Vos, 1999;
219 ten Cate, 2000; Payne, Payne & Woods, 1998; Payne *et al.*, 2000; Beltman, Haccou &
220 Ten Cate, 2003). (Fig. 1).

221 Here we are interested in the learning process of mating preferences, mainly by
222 females. This process adds phenotypic variability to the mate-choice behaviour within a
223 population, because every female has her unique experience with the environment.
224 Indeed, the behaviour of each female will be the outcome of her personal knowledge
225 (Danchin *et al.*, 2008; Wagner & Danchin, 2010), which is the sum of her independent
226 and non-independent information on which to base her mating decisions. Independent
227 information includes the female's genetic preferences, her preferences passively acquired
228 via sexual imprinting, and her preferences actively acquired via direct personal
229 experience with males (also known as within-generational learning; Dukas 2013;
230 Servedio & Dukas 2013). Non-independent information includes the female's indirect
231 experience with the mating behaviour of others, that is, without direct personal experience
232 with males, which can lead to mate-choice copying (Fig. 1).

233

234 **(2) What is mate-choice copying?**

235 Mate-choice copying is a non-independent mechanism of (mostly) female mate-choice.
236 It is a type of social learning and occurs when the mating preference of an observing

237 female for a particular male increases or decreases, depending on whether that male mated
238 previously or was avoided by another female (Wade & Pruett-Jones, 1990; Dugatkin,
239 1992; Pruett-Jones, 1992; Dugatkin, 1996a). This behaviour shows that female mating
240 preferences are not fixed throughout their lives, but that they can change via observing
241 other females' choices. In other words, it represents a shift or a novelty in an individual's
242 innate mate choice behaviour (Lindholm, 2015).

243 Mate-choice copying was originally proposed as an explanation for the marked
244 skews in male mating success observed in many lekking species (Bradbury, 1981;
245 Bradbury & Gibson, 1983; Losey *et al.*, 1986; Wade & Pruett-Jones, 1990; Gibson &
246 Höglund, 1992). It was first tested by Dugatkin (1992) and Dugatkin & Godin (1992),
247 using guppies *Poecilia reticulata* as models, and later by Galef & White (1998) using
248 Japanese quails *Coturnix japonica*. Subsequent field and laboratory studies found
249 evidence for copying in sailfin mollies *Poecilia latipina* (e.g. Schlupp *et al.*, 1994; Witte
250 & Ryan, 2002), ocellated wrasse *Symphodus ocellatus* (Alonzo, 2008), zebra finch
251 *Taeniopygia guttata* (e.g. Swaddle *et al.*, 2005), black grouse *Tetrao tetrix* (Höglund *et*
252 *al.*, 1995), house mouse *Mus musculus* (Kavaliers *et al.*, 2006) and humans (e.g.
253 Waynforth, 2007; Yorzinski & Platt, 2010). These are only a few of the many examples
254 that can be found in the literature (reviewed in Galef & White, 2000; Westneat *et al.*,
255 2000; Valone & Templeton, 2002, Vakirtzis, 2011 and Witte *et al.*, 2015), including the
256 first evidence of mate-choice copying in an invertebrate species, *Drosophila*
257 *melanogaster* (Mery *et al.*, 2009), and more recently in *Schizocosa* wolf spiders (Fowler-
258 Finn *et al.*, 2015). Finding mate-choice copying in invertebrates has considerable
259 importance because it indicates that copying could be widespread in nature, representing
260 a general rule, instead of being an exclusive ability of more complex cognitive systems,
261 such as those of vertebrates (Leadbeater, 2009).

Interestingly, the first studies on mate-choice copying (Bradbury, 1981; Bradbury & Gibson, 1983; Losey *et al.*, 1986; Wade & Pruett-Jones, 1990; Dugatkin, 1992; Dugatkin & Godin, 1992; Gibson & Höglund, 1992; Pruett-Jones, 1992; Galef & White, 1998) are contemporary to the first compelling studies supporting the genetic-based hypotheses of female mate choice (Lande, 1981; Andersson, 1982; Kirkpatrick, 1982; Majerus *et al.*, 1986; Majerus 1986; Andersson, 1994; Møller, 1994; Mead & Arnold, 2004), though the implications of mate-choice copying for the evolutionary mechanisms of sexual selection have not yet been given much attention.

(3) Why should females rely on copying?

Throughout their lives, females, in general, have fewer breeding opportunities than males, which typically makes them the choosier sex (Bateman, 1948). Yet, choosing the best partner, among the many potentially available, is not easy, and females, when choosing independently from each other, may make evaluation mistakes (Ryan, Akre & Kirkpatrick, 2007; Vakirtzis, 2011; Witte *et al.*, 2015).

According to the mate-choice copying theory, copying could have evolved as a direct adaptation to assess more effectively the quality of potential mates (Wade & Pruett-Jones, 1990; Gibson & Höglund, 1992; Pruett-Jones, 1992; Brooks, 1998; Nordell & Valone, 1998; Valone & Templeton, 2002; Danchin *et al.*, 2004; Dugatkin, 2005; Wagner & Danchin, 2010). The explanation given is that mate-choice copying is a type of inadvertent social information, meaning that the relevant information about the males is obtained from other females – whether they were accepted or rejected by those females (Danchin *et al.*, 2004; Wagner & Danchin, 2010). In other words, the information about males' mating performance does not involve active signalling by males and, consequently, cannot be manipulated by them. Moreover, because the environment is not

287 constant in space and time, male genetic characteristics may not always match up
288 correctly with their environment. Therefore, when different males succeed or fail in
289 mating with model females, the inadvertent information that they produce about their
290 success or failure will generally reflect male genetic differences in quality, providing
291 reliable and updated information about the males to the observer females (Danchin *et al.*,
292 2008).

293 This reasoning assumes that model females have enough personal knowledge
294 about male variability in quality so that they will make the right decision. If, however,
295 they lack that knowledge and mate with lower quality males, they will mislead the mate
296 choices of copying females. The outcome will, however, be no different as if copying
297 females would have chosen males randomly, so copying behaviour does not increase the
298 females' probability of making wrong choices (Nordell & Valone, 1998). Nonetheless,
299 mate-choice copying is thought to be prevalent in females with poor ability to
300 discriminate (Nordell & Valone, 1998), or when the cost of mate assessment is high
301 (Dugatkin, 2005). Such females are generally younger and inexperienced or are females
302 that had previous unsuccessful breeding attempts (Danchin *et al.*, 2008). Accordingly,
303 only older/experienced and high-quality model females are generally used as reliable
304 models from which to copy (Dugatkin & Godin, 1993; Amlacher & Dugatkin, 2005; Hill
305 & Ryan, 2006; Vukomanovic & Rodd, 2007; Waynforth, 2007; Yorzinski & Platt, 2010;
306 and see Vakirtzis, 2011 for a review). On the other hand, copying should increase in
307 frequency, in all types of females, if the discrimination task becomes more difficult,
308 which can happen when males are phenotypically quite similar (Dugatkin, 1996b; Nordell
309 & Valone, 1998; Witte & Ryan, 1998), or quite different (Mery *et al.*, 2009; see also
310 Smolla *et al.*, 2016) from each other.

311 Furthermore, mate-choice copying could reduce the time and energy invested into
312 the independent assessment of several potential mates (Wade & Pruett-Jones, 1990;
313 Gibson & Höglund, 1992; Pruett-Jones, 1992; Schlupp & Ryan 1996). By doing so, it
314 also reduces the costs of direct interactions with males, such as those from sexual
315 harassment, sexually transmitted diseases, parasite exposure and vulnerability to
316 predation (Pomiankowski, 1987, Reynolds & Gross, 1990, Andersson, 1994; Dugatkin &
317 Höglund, 1995; Dugatkin, 2005).
318 Mate-choice copying theory thus predicts that the use of social information may
319 be both a cost effective and reliable approach to mate choice. Theoretical models have
320 shown that when the cost of choosing is high, it increases the adaptive advantage of the
321 copying strategy (Pruett-Jones, 1992; Dugatkin & Hoglund, 1995; Dugatkin, 2005;
322 Brennan, Flaxman & Alonzo, 2008). However, from an empirical point of view, there is
323 still no evidence supporting the cost avoidance advantage of mate-choice copying
324 (Briggs, Godin & Dugatkin, 1996; Dugatkin & Godin, 1998, but see Vakirtzis, 2011).
325 Regarding the role of copying in facilitating male quality assessment and discrimination,
326 the theoretical (Losey *et al.*, 1986; Servedio & Kirkpatrick, 1996; Stöhr, 1998; Sirot,
327 2001; Uehara, Yokomizo & Iwasa, 2005) and empirical record (reviewed in Vakirtzis,
328 2011 and Witte *et al.*, 2015) are vast.
329
330 **(4) Why does mate-choice copying matter to evolution?**
331 Mate-choice copying can have evolutionary consequences when it gives rise to stable
332 informational cascades and if it is followed by the social generalisation of the learned
333 mating preferences. The concept of informational cascade has been proposed by
334 Bikhchandani, Hirshleifer & Welch (1992; 1998) to explain localized conformity and
335 fragility of mass behaviour in humans, but may also apply to mate-choice copying

(Gibson & Höglund, 1992; Giraldeau, Valone & Templeton, 2002; Kendal *et al.*, 2005; Rieucau & Giraldeau, 2011). The model posits that any behaviour can spread rapidly through a population with a single individual as the starting point if observers copy the relevant behaviour. Informational cascades could either propagate accurate or erroneous mating decisions. This is possible, because mate-choice copying, as it is defined (Pruett-Jones, 1992), is based not on the courtship signalling of males towards the model females, but on the outcome of those interactions, i.e., on the social cues that are inadvertently produced by the mating decisions of model females (Danchin *et al.*, 2004). And when the key information is the behavioural decision of the demonstrator individual (accepting or rejecting to mate with a certain male) and not the actual information on which the demonstrator based her decision (the male courtship behaviour), erroneous information can be transmitted (Bikhchandani *et al.*, 1992; Gibson & Höglund 1992; Dugatkin 1996a; Bikhchandani *et al.*, 1998; Giraldeau *et al.*, 2002; Kendal *et al.*, 2005; Rieucau & Giraldeau, 2011). If, however, an informational cascade is based on accurate information on mate quality, informational cascades will help spread the learned behaviour throughout the population of potential copiers. There is evidence that animals engage on informational cascades in the context of food choice (e.g. Aplin *et al.*, 2015; and see reviews in Giraldeau *et al.*, 2002; Kendal *et al.*, 2005; Rieucau & Giraldeau, 2011). However, no informational cascade on mate choice copying has yet been formally tested, though theoretical work assumes the informational cascade process when copier individuals become demonstrators themselves (e. g. Kirkpatrick & Dugatkin, 1994; Laland, 1994; Agrawal, 2001; Santos *et al.*, 2014).

Social generalisation, on the other hand, occurs when the observer female learns to copy the choice of the male phenotype by the demonstrator female and not necessarily or exclusively the choice of the individual male (Brooks, 1998). This means that the entire

population of copied individuals, the males, will be affected by such a shift or novelty in female mating behaviour. There is empirical evidence of mate-choice copying generalization for new male ornaments in four vertebrate species: Japanese quails (White and Galef, 2000), guppies (Godin, Herdman & Dugatkin, 2005), mollies (Witte & Noltemeier, 2002) and zebra finches (e.g. Drullion & Dubois, 2008), but also in fruit flies (Mery *et al.*, 2009).

When informational cascades and social generalization of preferences are in place, mate-choice copying acquires the potential to modify the selection pressures for the preferred male traits, changing the rate and direction of sexual selection (Kirkpatrick & Dugatkin, 1994; Laland, 1994a; Agrawal, 2001; Danchin & Wagner, 2008; Danchin & Wagner, 2010; Santos *et al.*, 2014; Witte *et al.*, 2015). For that reason, it has been hypothesised that mate-choice copying could have favoured the emergence of new species, by inducing reproductive isolation between individuals with different copying traditions (e.g. Gibson & Höglund, 1992; Witte & Noltemeier, 2002; Danchin *et al.*, 2004; Danchin & Wagner, 2008; Leadbeater, 2009; Mery *et al.*, 2009; Fowler-Finn *et al.*, 2015). Copying has thus been seen as an additional mechanism to the diversification of species.

Surprisingly, however, the hypothesis has never been fully formalised. It is presented as a very straightforward prediction of empirical findings in mate-choice copying studies. Such findings are said to have «implications for evolution given that socially learned mate preferences may lead to reproductive isolation, setting the stage for speciation» (Mery *et al.*, 2009; see also Danchin *et al.* 2004; Leadbeater, 2009; Fowler-Finn *et al.* 2015). Such a prediction is indeed very intuitive and powerful. However, put this way, it is too simplistic. The hypothesis needs a much deeper reflection of its assumptions and predictions. Besides, as we propose here, mate-choice copying may also merge different behavioural phenotypes into one, leading conspecific and heterospecific

386 populations to hybridise. In the next sections, we will provide such thorough reflection
387 on the role of mate-choice copying to both speciation and hybridization.
388
389
390 **III. THE ROLE OF MATE-CHOICE COPYING IN SPECIATION**
391 **(1) When, within a population (in sympatry), copied preferences diverge from each**
392 **other**
393 The hypothesis that mate-choice copying can cause species fission, describes a scenario
394 of sympatric speciation, where copied preferences contradict a certain proportion of the
395 females' population that, with no more information available, would have chosen males
396 based on their innate preferences or individual experience (Mery *et al.*, 2009; Leadbeater,
397 2009; Fowler-Finn *et al.* 2015; see also Danchin *et al.* 2004). For instance, it is known
398 that, in guppies, females have a genetic preference for males with large areas of orange
399 pigment in their colour patterns (Houde, 1987; Houde, 1988; Dugatkin, 1996b). There is,
400 however, within and between population variation in the degree of female preference for
401 orange (Houde & Endler, 1990) and also limited time and energy for females to assess
402 every male in a population (Endler, 1983). This makes it possible that if a new male
403 phenotype, with smaller orange areas, enters a population (by migration or mutation) a
404 number of females may choose the new phenotype. Knowing, additionally, that there is
405 mate-choice copying in this species (e.g., Dugatkin, 1992; Dugatkin & Godin, 1992;
406 Dugatkin, 1996b; Amlacher & Dugatkin, 2005; Dugatkin & Godin, 1993; Goding & Hair,
407 2009), it means that a proportion of the females' population will rely on the choices of
408 other females. This has been shown by Dugatkin (1996b), where observer females copied
409 the mate choice of model females for males with smaller orange areas in their colour
410 patterns. Hence, if some of the females choose males with smaller orange areas, this could

411 trigger an alternative informational cascade to that of the choice of males with larger
412 orange areas (Bikhchandani *et al.*, 1992; Dugatkin, 1996b), causing a behavioural
413 divergence within the population. But would this set the stage to reproductive isolation
414 and ultimately speciation under sympatry?

415 We think not. First of all, and according to speciation theory (Mayr, 1963;
416 Arnegard & Kondrashov, 2004; Coyne & Orr, 2004; Butlin, Bridle & Schluter, 2008;
417 Nosil, 2012), it is unclear whether sympatric speciation can occur via behavioural
418 isolation. In general, sexual selection is thought to have only a small impact in the early
419 stages of speciation (Streelman & Danley, 2003; Arnegard & Kondrashov, 2004). Genetic
420 models of sexual selection predict sympatric speciation only if few genes are involved in
421 female preference and male display traits and if there is symmetric assortative mating
422 regarding those traits. Otherwise, the tendency would be for directional selection, with
423 the loss of genetic variability (Arnegard & Kondrashov, 2004). Such complex scenarios
424 are thought to be very rare in nature (Via, 2001; Kraaijeveld's *et al.*, 2011), suggesting
425 that early divergence in the ecological needs of both populations (ecological speciation)
426 is a necessary ingredient to consistently reduce gene flow among them and avoid
427 competitive exclusion (Coyne & Orr, 2004; Nosil, 2012). Disruptive sexual selection will
428 probably act only later, reinforcing the process of reproductive isolation that is already in
429 place by disruptive natural selection (Streelman & Danley, 2003; Arnegard &
430 Kondrashov, 2004). This seems to be the evolutionary scenario of the best-recognized
431 examples of sympatric speciation (smelt fish *Osmerus*, Taylor & Bentzen, 1993; Crater
432 Lake cichlids, Schliewen, Diethard & Pääbo, 1994; Lake Tana large barbs, Mina,
433 Mironovsky & Dgebuadze, 1996; sock-eye salmon *Oncorhynchus nerka*, Wood & Foote,
434 1996; apple maggot *Rhagoletis pomonella*, Filchak, Roethele & Feder, 2000).

435 Secondly, copying females can obtain their information from any other females
436 in the population, and most likely from unrelated model females. In fact, one of the
437 important characteristics of non-genetic information is that it can be transmitted in all
438 three directions: vertical, horizontal and oblique (Danchin & Wagner, 2010; Danchin *et*
439 *al.*, 2011; Danchin, 2013). Mate-choice copying is not an exception (Danchin *et al.*,
440 2004). Therefore, any type of linkage disequilibrium between the learned preference
441 (non-genetic information) and the male trait (genetic information) will be disrupted when
442 the information inheritance is not vertical. Yet, speciation with gene flow and without
443 linkage disequilibrium has been found theoretically unlikely (e.g. Felsenstein, 1981;
444 Arnegard & Kondrashov, 2004; Verzijden *et al.*, 2005), and is subject to debate (Via,
445 2001; Kraaijeveld's *et al.*, 2011). Indeed, in models where different inheritance
446 mechanisms of mate choice were tested (Verzijden *et al.*, 2005; Servedio, Sæther &
447 Sætre, 2009), the copying scenario (that the authors modelled as oblique sexual
448 imprinting) did not succeed in causing disruptive divergence in sympatry. This was not
449 the case for maternal imprinting because that information runs between related
450 individuals – females learn from their mothers – and the linkage disequilibrium between
451 the genomes of the females that learn and the genomes of the male traits is preserved.
452 Verzijden & ten Cate (2007) provided an empirical example of how sexual imprinting
453 seems to have participated in the reproductive isolation of a species pair of African
454 cichlids in Lake Victoria.

455 Thirdly, theoretical models have been studying the ways in which mate-choice
456 copying can help the spread of novel male traits in a population (Kirkpatrick & Dugatkin,
457 1994; Laland, 1994a; Agrawal, 2001; Santos *et al.*, 2014), potentially affecting its genetic
458 variability and rate of divergence. However, all models agree that copying is strongly
459 affected by a positive-frequency dependent advantage of the most common male

460 phenotype – *conformity to the majority* rule (Bikhchandani *et al.*, 1998; Fig. 2) – that
461 prevents the spread of novel (by mutation or migration) male trait alleles in a population
462 by mate-choice copying (Kirkpatrick & Dugatkin, 1994; Laland, 1994; Agrawal, 2001;
463 Santos *et al.*, 2014). Novel traits are rare in the first generations and so only a few females
464 will be observed mating with these males, which will generate very few positive
465 information about them. Moreover, if the novel trait provides a competitive advantage or
466 courtship vigour to the males, or explores a female sensory bias, it can rapidly spread and
467 achieve fixation without the need for copying (Santos *et al.*, 2014). This means that a
468 mate-choice copying informational cascade favouring the most common phenotype (the
469 phenotype with the larger orange area in the guppy example) would prevent the
470 establishment of the information pathway for males with the new phenotype (smaller
471 orange areas), hampering disruptive sexual selection.

472 However, copying could still have an effect on the spread of novel male traits, but
473 only if females are more strongly influenced by the observation of successful matings
474 with novel males than by the observation of successful matings with common males. This
475 could generate directional selection towards the novel male trait – *attraction to novelty*
476 rule (Fig. 2) –, as was shown by Agrawal's (2001) mathematical model, but not disruptive
477 sexual selection.

478 More recently, Santos *et al.* (2014) have included into their mathematical model
479 another important element of mate-choice copying theory, which is the transmission of
480 negative information about males. When females observe model females accepting to
481 mate with certain types of males, the inadvertent social information that the males will be
482 producing about their performance is positive information. However, model females also
483 reject males and, in this case, the males would be inadvertently advertising their lack of
484 success. It has been demonstrated empirically that females do actually copy male rejection

485 (Witte & Ueding, 2003) and Santos *et al.* (2014) have shown that by incorporating
486 negative information in the simulated population, the positive-frequency dependence
487 favouring the most common phenotype loses strength (because many more common
488 males are observed being rejected than rare males) and so the novel trait, when associated
489 with male vigour, may spread in the population by mate-choice copying and achieve
490 fixation (though that would occur without mate-choice copying, anyway). In this case,
491 females would be incorporating in their decisions the complete information about the
492 males' mating performance – *appreciation of performance* rule (Fig. 2) – as mate-choice
493 copying theory predicts (Pruett-Jones, 1992; Danchin *et al.*, 2004; Santos *et al.*, 2014),
494 instead of relying exclusively on conformity (that only takes positive information into
495 account), or novelty (that gives more weight to positive information by males with rare
496 phenotypes).

497 Nonetheless, whatever the mate-choice copying rule applied, the outcome of
498 mathematical simulations is the fixation of one of the alleles. This way, mate-choice
499 copying does not contribute to the evolution of divergence, in sympatry, between the two
500 male phenotypes (of large and small orange areas in the guppy example), but to
501 directional selection instead. This leads to the loss of male polymorphisms, in the absence
502 of which sympatric speciation cannot occur (Verzijden *et al.*, 2005; Servedio *et al.*, 2009;
503 Fig. 2).

504

505 **(2) When, between populations in micro-allopatry, copied preferences diverge from**
506 **each other and facilitate reproductive isolation**

507 In complex and dynamic environments, habitat conditions differ and change rapidly
508 across space and time. It thus has been recently recognized that such ecological
509 complexity affects the dynamics of sexual selection (Cornwallis & Uller, 2010; Miller &

510 Svensson, 2014), creating a mosaic of female preferences and male sexual traits (Gosden
511 & Svensson, 2008), where genotype-by-environment interactions set the stage for local
512 adaptation (Ingleby, Hunt & Hosken, 2010). Mate-choice copying is more likely to have
513 a role in speciation under such a fine-grained mosaic scenario, such as a situation of
514 micro-allopatry, with early stages of reproductive isolation caused by ecological
515 divergence (Streelman & Danley, 2003; Arnegard & Kondrashov, 2004; Coyne & Orr,
516 2004; Nosil, 2012), than under a scenario of full sympatry. This is represented in the first
517 scenario of Fig. 3 and in Fig. 4.

518 In micro-allopatry, when populations are structured via habitat selection, with
519 divergent adaptation to local conditions (micro-ecological barriers, with micro-spatial
520 variation), mate-choice copying can have a role in further divergence via a positive-
521 frequency dependent effect towards the more common male (Kirkpatrick & Dugatkin,
522 1994; Laland, 1994a; Agrawal, 2001; Santos *et al.*, 2014) – the conformity to the majority
523 rule. This is likely because it would preserve the phenotypes of the local males –
524 independently of whether they perform better or worse than migrant males –, facilitating
525 reproductive isolation between patches. Additionally, if local males perform better than
526 migrating ones and the appreciation of performance rule applies, local females would
527 mate more often with local males than with migrating ones, which would also facilitate
528 directional selection towards local males. (The attraction to novelty rule does not apply
529 here, because under this rule the copied preferences between patches will agree with each
530 other, promoting convergence of preferences instead of divergence; see in the next section
531 and in the third scenario of Fig. 3). This would only be true, however, if only local females
532 are prone to copy. Migrant females should either remain faithful to migrant males (via
533 maternal sexual imprinting that they bring with them as they were raised in a different
534 patch) or do not migrate at all (via male sex-biased dispersal). Otherwise, conspecific

hybridization between migrant females and local males would not be avoided, leading to genetic introgression and hence disrupting the genetic divergence between patches promoted by local females.

Hence, mate-choice copying might not be at the origin of speciation in scenarios of sympatry, but can have a facilitating role in the subsequent process of divergence in micro-allopatry, by conditioning local (but not migrant) females, to certain mate choices locally. By doing so, mate-choice copying will help to create different canalised female preference phenotypes in each habitat patch and cause disruptive sexual selection for male traits between patches. This will ultimately facilitate species' fission. However, if conspecific hybridization between migrant females and local males is not avoided, it would be difficult to predict how much a facilitator of divergence mate-choice copying might be.

The recent finding that great tits use social learning to acquire novel foraging techniques and that they retain the tradition that is most common to their population, or, even more remarkable, adopt the local tradition when dispersing to neighbouring populations via the behavioural process of social conformity (Aplin *et al.*, 2015), is a strong example of how copying behaviour can indeed condition the prevailing behaviour in an entire population and cause divergence of preferences between habitat patches. This leaves the suggestion that copying foraging techniques could initiate a process of local adaptation, to which mate-choice copying could subsequently add a second selective force. Examples like this are scarce in the published literature, but we recognise that this is not easily tested empirically. On the other hand, theoretical models could much more easily consider the joint actions of ecological divergence and mate-choice copying, as well as of foraging and habitat copying with mate-choice copying.

(3) When, between populations in allopatry, copied preferences diverge from each other and reinforce or accelerate reproductive isolation

This scenario describes the divergence process at a larger scale, between populations that have been evolving in allopatry or have recently become isolated. Here, the same reasoning of habitat structuring and adaptation to local conditions, as those describe in the previous section, applies. Under those conditions, mate-choice copying could reinforce or accelerate the speciation process by introducing or strengthening the mechanism of behavioural isolation. This corresponds to the second scenario in Fig. 3. All copying rules apply here (Fig. 5): with conformity to the majority, males of the most common phenotype in each population will be favoured and copying will help the corresponding male trait alleles to reach fixation; with appreciation of performance, the best performer males and their alleles – which will depend on environmental conditions and vary between populations – will be favoured; and with attraction to novelty, it will be the males with the new phenotypes that will be preferred. In this case, the new phenotypes will independently arise in each population by mutation instead of migration.

Consider, for instance, in the guppy example, two isolated populations: one occupying a location with high predation risk and the other a location with low predation risk. In the first one, males with small areas of orange are in advantage because they are less visible to predators (Endler, 1983). Choosing less orange males would be adaptive to females in those circumstances, though males with large areas of orange are generally more attractive to them (Endler, 1983; Dugatkin, 1996b). Mate-choice copying could reinforce the speciation process between the two populations, by creating an informational cascade favouring the less orange males in the population with high predation risk, either because, under those circumstances, less orange males are more abundant or perform better. This phenotypic plasticity provided by mate-choice copying

could make a difference, indeed, because it would probably take a while until the adaptive genetic change in female preference for males with small orange areas will appear in the population. Mate-choice copying can accelerate that change in females' behaviour and accelerate speciation as a by-product, contributing to fixation of the male trait allele and the female preference allele once the mutation appears. Moreover, mate-choice copying will allow the population to survive until the mutation's emergence. Otherwise, the population would go extinct due to predation pressure. On the contrary, if females never change genetically to prefer males with small orange areas, and if the geographical barrier is destroyed at some point in time, the mate-choice copying effect will be reversed due to introgression between the two populations, or the rules of the previous section will apply. Hence, again, mate-choice copying should not be seen as a cause for speciation, but as a secondary vehicle by which speciation could be achieved.

(4) When, between populations in micro-allopatry, copied preferences agree with each other and prevent reproductive isolation

This is represented in the third scenario of Fig. 3 and in Fig. 6. It describes the cases where there is no divergence of the copied preferences between populations under micro-allopatry, but convergence instead. If the copying rule is attraction to novelty (Agrawal, 2001), local females will be more strongly biased to mate with migrant males when they observe them mating than are females that observe local males mating. By the same reasoning, migrant females will be more biased to mate with local males. Put together, the two effects result in the constant mixing of phenotypes among habitat patches, preventing reproductive isolation between them. On the other hand, if there is a male phenotype that more frequently migrates, attraction to novelty would alternatively canalise selection towards a unique male phenotype among patches. Additionally, if

610 migrants from one of the neighbouring patches perform better than local males in the
611 remaining patches and the appreciation of performance rule applies, local and migrant
612 females will both copy migrant males more often than local males, again canalising
613 selection towards one male phenotype, preventing reproductive isolation between
614 patches. (Here, the majority to the conformity rule does not apply because under this rule
615 local and migrant females would be both biased towards local males, promoting
616 divergence between patches instead of convergence; see in the previous section and in
617 the first scenario of Fig. 3).

618 Interestingly, the loss of male polymorphisms among patches by mate-choice
619 copying when there is a convergence of preferences is achieved at a slower rate than in
620 an evolutionary model without copying (Santos *et al.*, 2014). In fact, according to Santos
621 *et al.* (2014), mate-choice copying seems «to have a more conservative role in the
622 evolution of male traits, by reducing the strength and direction of selection» (Santos *et*
623 *al.*, 2014). Expressed in another way, we could say that mate-choice copying delays the
624 loss of genetic variability, which could give a population increased or decreased chances
625 of survival under environmental change.

626 Sexual selection has, for instance, been suggested to increase species' extinction
627 rate (Promislow, Montgomerie & Martin, 1992; Tanaka, 1996; Kokko & Brooks, 2003;
628 but see Lumley *et al.* 2015), which could explain why there is less evidence for speciation
629 by sexual selection than by ecological divergence (Kraaijeveld's *et al.*, 2011). Several
630 mechanisms could operate independently, namely the trade-off between male mating
631 success and viability (Kokko & Brooks, 2003), where males with extreme traits are
632 preferred by females, experiencing higher mating success, but then paying the cost of
633 decreased viability. The paradigmatic example is that of the Irish elk (*Megaloceros*
634 *giganteus*), which is thought to have been extinct due to its gigantic antlers. The energetic

requirements for antler growth were probably incompatible with poorer environmental conditions due to climate change (e.g. Moen, Pastor & Cohen, 1999). With a mathematical model, Kokko & Brooks (2003) arrived at similar predictions: in variable environments, extreme ornaments lead a population to extinction if the extreme male trait allele reaches fixation before the environmental change happens (Kokko & Brooks, 2003). Mate-choice copying, by delaying the loss of male polymorphisms, would be allowing a population to cope better with environmental changes because the population would include males with alternative phenotypes for a larger number of generations. If, on the other hand, the male trait increases viability, mate-choice copying, by delaying the loss of male polymorphisms and hence the fixation of the favourable trait, would also delay the population's short-term response to environmental change (evolutionary rescue, Carlson, Cunningham & Westley, 2014), putting the population at risk. A new mathematical model, similar to that of Kokko & Brooks (2003), simulating trade-offs between male mating success and viability, could easily incorporate mate-choice copying to test its impact on species extinction risk either when new male traits increase or decrease viability. This effect is compatible with the role of learning in phenotypic plasticity (Verzijden *et al.*, 2012), as plasticity gives a species increased resilience to environmental change (Canale & Henry, 2010) and behavioural plasticity could, in fact, have an impact on the speed of evolution (Price, Qvarnstrom & Irwin, 2003; Duckworth, 2009).

IV. THE ROLE OF MATE-CHOICE COPYING IN HYBRIDIZATION

Additionally to the traditional view that mate-choice copying can favour the emergence of new species, we propose a new hypothesis that mate-choice copying may also have the

potential to direct sexual selection towards interspecific hybridization if individuals from distinct species copy each other's mate choice. In other words, hybridization may be facilitated when between species in secondary contact copied preferences agree with each other. If copying has the potential to facilitate or reinforce speciation via divergent mate preferences with conspecifics (scenarios 1 and 2 in Fig. 3), or prevent speciation via convergent mate preferences with conspecifics from different populations (scenario 3 in Fig. 3), why should not the same behaviour under the right circumstances promote hybridization via convergent mate preferences with heterospecifics (scenario 4 in Fig. 3)?

Interspecific hybridization is common in nature, occurring in at least 10 % of animal species (Coyne & Orr, 2004; Mallet, 2004; Seehausen, 2004; Mallet, 2007; Grant & Grant, 2008). It occurs when the mechanisms of species recognition are incomplete (Burdfield-Steel & Shuker, 2011). Incomplete recognition is common between species that had only recently diverged. It is also possible between allopatric species that had diverged ecologically for long periods of time, but without developing behavioural isolation (Coyne & Orr, 2004; delBarco-Trillo & Johnston, 2010; Weissing, Edelaar & Van Doorn, 2011; Abbott *et al.*, 2013). In either case, when species meet under secondary contact, they will still see each other as good-quality mates – heterospecific mating signals are interpreted as good-quality ones – leading males to court heterospecific females and females to accept matings from heterospecific males (Mendelson & Shaw, 2012). This may eventually produce hybrids that could be successful or unsuccessful depending on the strength of postzygotic barriers (Coyne & Orr, 2004; Fig. 1). Under these conditions of incomplete recognition systems, mate-choice copying may promote hybridization even further, as it can lead females from different species to learn from each other, that is, to interpret the mating decisions of heterospecific females as good-quality ones. This will induce "erroneous" informational cascades, speeding up the spread of

685 social information that mating with heterospecifics is at least as good as mating with
686 conspecifics. This is likely under the mate-choice copying theory, because it is when
687 females lack the ability to discriminate between males – in this case, when females lack
688 a complete recognition system – that mate-choice copying is most likely to be utilized by
689 choosing females (Nordel & Valone, 1998; Mery *et al.*, 2009).

690 Hence, the mechanisms by which mate-choice copying can cause hybridization
691 are similar to those described for speciation but dependent upon the species recognition
692 abilities and the circumstances under which they came into secondary contact. If
693 secondary contact is caused by migration, and heterospecific males are seen as poor-
694 quality mates, neither local nor migrant females will mate with heterospecific males and,
695 consequently, no hybridization will occur between the two species. If, on the other hand,
696 heterospecific males are seen as good-quality mates (Fig. 7), hybridization may occur
697 with and without mate-choice copying, but mate-choice copying will have a facilitator
698 role. This role could be particularly relevant if females are still more attracted to
699 conspecific males than to heterospecifics – despite the incomplete recognition system –
700 since mate-choice copying will increase the attractiveness of heterospecific males. If the
701 conformity to the majority rule applies, mate-choice copying will, however, only facilitate
702 hybridization of migrant females with local males and inhibit hybridization of local
703 females with migrant males, due to positive frequency-dependence favouring the local
704 males. On the other hand, when the copying rule favours the use of both positive and
705 negative information about males' performance – the appreciation of performance rule –
706 migrating males may be considered more attractive than locals if they perform better, or
707 less attractive if they perform worse. In the first case, both local and migrant females will
708 mate with migrant males, since migrant females will reinforce their preference for
709 conspecific males; in the second case, migrant females will hybridise with local males

710 and the local females will reinforce their preference for conspecific males. Finally, if the
711 copying rule favours the new male phenotype – the attraction to novelty rule –, both local
712 and migrant females will hybridise. This same reasoning can be applied to when
713 secondary contact is caused by the overlap of the species' ranges. In this case, the number
714 of encounters with heterospecifics could be considerably higher, along with mate-choice
715 copying effects.

716 Hybridization is one of the phenomena that strongly contributes to biodiversity
717 changes (Seehausen, 2004; Mallet, 2005; Mallet, 2007; Nolte & Tautz, 2010; Abbott *et*
718 *al.*, 2013). At the proximate level, it can act against differentiation due to the breakdown
719 of reproductive barriers, which reduces species diversity by merging previously
720 distinctive evolutionary lineages, leading sometimes to the extinction of populations or
721 species (Todesco *et al.*, 2016). On the other hand, hybridization may increase the gene
722 pool of the mixed populations and consequently their chances of adaptation to novel or
723 changing environments (Seehausen, 2004; Mallet, 2005; Mallet, 2007; Grant & Grant,
724 2008; Nolte & Tautz, 2010; Bourne *et al.*, 2014). This can be achieved by creating stable
725 hybrid zones (Buerkle, Wolf & Rieseberg, 2003), or leading to the genetic rescue of small
726 inbred populations (Johnson *et al.* 2010; Carlson *et al.*, 2014). Ultimately, hybridization
727 can even reinforce reproductive isolation if there is selection against hybrids and
728 hybridization is not so common (Abbott *et al.*, 2013; Todesco *et al.*, 2016). Or it can
729 originate new reproductive isolation by the instantaneous formation of new hybrid
730 lineages, or by causing adaptive introgression of new traits that could lead to adaptive
731 radiation. This would be the case if the hybrid populations gain the necessary genetic
732 tools to rapidly adapt to environmental conditions that were previously inaccessible to the
733 parental species (Mallet, 2005; Mallet, 2007; Salazar *et al.*, 2010; Butlin *et al.*, 2012;
734 Abbott *et al.*, 2013; Seehausen, 2013). The outcomes of hybridization by mate-choice

copying are no different from these: it can cause fusion of species, by creating or maintaining hybrid zones (scenario 4a in Fig. 3); it can contribute to the success of novel lineages (scenario 4b in Fig. 3); or if hybridization costs are involved, it can cause reproductive interference and increase species extinction risk, which then could reinforce or preserve already existent reproductive isolation (scenario 4c in Fig. 3). In the next sections, we will outline each one of these scenarios.

(1) When, between species in secondary contact, copied preferences break down reproductive isolation

When hybridization occurs and there is a certain degree of hybrid viability, either developmental or ecological (Fig. 1), mate-choice copying, as a promoter of hybridization, will merge different behavioural phenotypes into one, contributing to the creation or maintenance of hybrid zones. This could eventually lead to species fusion, recovering, via adaptive introgression, intra-population genetic variability and producing highly plastic behavioural phenotypes that will be better in coping with environmental changes (scenario 4a in Fig. 3).

A well-known example of a hybrid zone is that between the two subspecies of house mice, *Mus musculus musculus* and *Mus musculus domesticus*. The subspecies are found across Europe and Northern Asia, and their ranges overlap in Central Europe, with the formation of the hybrid zone that spans from Denmark to Bulgaria (Boursot *et al.*, 1993). It has been shown that *M. m. musculus* females generally prefer males from their own subspecies and that *M. m. domesticus* females do not discriminate between both (Zinck & Lima, 2013). Hence, the hybrid zone could be the result of *M. m. domesticus* females' inability to recognise their own subspecies. Additionally, if they rely on learning to decide with whom to mate, it creates opportunities for mate-choice copying. It has been

760 shown, indeed, that the laboratory CF-1 albino strain of house mice has the ability to
761 mate-choice copy (Kavaliers *et al.*, 2006). This study is a case of conspecific copying but
762 suggests an important role of this type of learning in the mating behaviour of the house
763 mouse. The question is how often the two subspecies could hybridise by mate-choice
764 copying. It will depend on how often they actually meet in the contact zone, on the
765 copying rule and in the relative abundance of each subspecies. It is possible that *M. m.*
766 *domesticus* is more abundant in certain areas of the contact zone and *M. m. musculus* in
767 others. If *M. m. domesticus* females conform to the majority, they will then copy the
768 choices of the most abundant population and, hence, more opportunities for hybridization
769 will exist if the *M. m. musculus* population is more abundant. If they are attracted to
770 novelty, they will copy the choices of the less abundant population and, hence, more
771 opportunities for hybridization will exist if *M. m. musculus* is less abundant. Finally, if
772 one type of male performs better than the other and if *M. m. domesticus* females rely on
773 performance, they will learn to copy the best performers in each location, regardless of
774 each subspecies relative abundance. All copying rules described in Fig. 7 could, therefore,
775 operate. Heterospecific mate-choice copying experiments between the two subspecies
776 would be necessary to test these hypotheses.

777 After hybridization events, the introgression of alleles from one of the species
778 involved into the gene pool of the other, and vice versa, becomes possible if hybrids mate
779 with the parental species. This process is adaptive if the introgressed alleles are favoured
780 by selection, which has indeed been demonstrated for the house mouse (Staubach *et al.*,
781 2012). Adaptive introgression has also been thoroughly studied by Grant & Grant (2008)
782 in the sympatric species of Darwin's ground finches, namely in *Geospiza fortis* and *G.*
783 *scandens.* They live on the island of Daphne Major in the Galapagos archipelago.
784 Hybridization, though apparently rare, has been present across the species' evolutionary

785 history, contributing to persistent genetic introgression. It is the result of sexual
786 imprinting of one species on the song of the other species. Since females mate according
787 to song type, misimprinted females will then mate with the wrong species, producing
788 hybrids. Hybrids themselves also mate according to song type, thus mating with the
789 paternal species. The resulting introgression increases the phenotypic and genotypic
790 variation of the backcrossed populations that gains the ability to explore environmental
791 conditions that were inaccessible to the parental species. This way, the backcrossed
792 populations can more rapidly respond to the challenge of environmental change than if
793 the two parental species were fully genetically isolated, setting the stage to adaptive
794 radiation (Grant & Grant, 2008; Seehausen, 2004). The question is whether mate-choice
795 copying, besides sexual imprinting, can also facilitate hybridization between two species
796 under similar circumstances. If this is the case, and given that mate-choice copying causes
797 informational cascades, the resulting hybridization events would be more common than
798 those from imprinting mistakes. This would increase the rate of adaptive introgression
799 between the species involved. Hybridization events will typically have very low impact
800 on the genetic architecture of a species (Abbott *et al.*, 2013). But if hybridization occurs
801 with a certain frequency among closely related species, the probability that one of those
802 events will contribute to adaptive introgression is higher (Abbott *et al.*, 2013). Mate-
803 choice copying might operate exactly here, by increasing the number of hybridization
804 events and by consequence the opportunities for adaptive introgression.

805 When hybridization is adaptive, it may also be facultative. This is the case of
806 spadefoot toads, *Spea bombifrons* and *Spea multiplicata*, which actively hybridise when
807 the habitat conditions are favourable to hybrid offspring (Pfenning, 2007). This behaviour
808 is asymmetric, i.e., hybridization is more common and more advantageous to *S.*
809 *bombifrons* females than to *S. multiplicata* females. Metamorphosis of *S. bombifrons*

tadpoles is slower and consequently they risk not achieving adulthood if developing in shallow ponds that dry quickly. By hybridising with *S. multiplicata* males, *S. bombifrons* females will produce hybrid tadpoles that develop faster than non-hybrids, which compensates for their lower fertility. Such facultative context-dependent female mate choice behaviour apparently does not have an underlying genetic mechanism, or there is still no evidence that it exists (Reyer, 2008). An alternative hypothesis is that of a learning mechanism, with facultative mate choice being either dependent on trial-and-error learning, or on mate-choice copying. If copying is involved, facultative mate choice could, therefore, be the result of inexperienced females copying the mate choices of older model females that by their previous breeding experience have better knowledge of their environment and thus can more reliably predict breeding success. This is exactly why mate-choice copying is thought to be adaptive (Nordell & Valone, 1998; Danchin *et al.*, 2004; Vakirtzis, 2011). A mate-choice copying experiment might not be difficult to conduct in these species and would allow testing this hypothesis.

(2) When, between species in secondary contact, copied preferences originate or facilitate reproductive isolation

When hybridization is successful (Fig. 1), besides breaking down reproductive isolation in the short-term, in the long-term it can also act as an additional source of differentiation between populations, originating new reproductive isolation (Mallet, 2007; Salazar *et al.*, 2010; Butlin *et al.*, 2012; Abbott *et al.*, 2013; Seehausen, 2013). In fact, the accumulation of genetic incompatibilities between populations of the same species that would lead to reproductive isolation, occurs generally too slowly to be able to explain all speciation events, namely by ecological divergence (Rundle & Nosil, 2005; Grant & Grant, 2008). Hybridization between related species can act as an additional mechanism of divergence

– an alternative to mutation – and may be more common than previously appreciated (Grant & Grant, 1994; Kim & Rieseberg, 1999; Arnold & Martin, 2009; Whitney, Randell & Rieseberg, 2010; Kunte et al., 2011, Abbott et al., 2013; Seehausen, 2013). This could be achieved as a result of adaptive introgression, adaptive radiation, or even hybrid speciation (Seehausen, 2004; Abbott et al., 2013; Seehausen, 2013). The role of mate-choice copying in promoting hybridization and, by consequence, in originating or facilitating reproductive isolation is described in scenario 4b of Fig. 3. Examples of hybridization by mate-choice copying that could result in adaptive introgression and adaptive radiation were given in the previous section. Regarding hybrid speciation, there is the interesting case of the Amazon molly species' complex, which is the only example in the literature of mate-choice copying involving different species.

The Amazon molly (*Poecilia formosa*) is a gynogenetic species and a case of hybrid speciation. It is an all-female fish that reproduces clonally. However, to initiate embryogenesis, the species relies on sperm from males of several heterospecific species, including its parental species, the sailfin molly (*P. latipinna*) and the Atlantic molly (*P. mexicana*). Heterospecific matings are therefore obligatory for the gynogenetic females to persist in nature (Schlupp, 2005). Interestingly, Schlupp *et al.* (1994) found that mate-choice copying occurs between Amazon and sailfin mollies, with sailfin males becoming more attractive to their conspecific females after having mated with the Amazons. The same was later confirmed for Atlantic mollies (Heubel *et al.*, 2008). In other words, heterospecific Amazon females are seen by sailfin and Atlantic females as reliable models to copy. Though this study is not a case of true heterospecific mate-choice copying (sailfin females did not learn to prefer Amazon males, and could not, because there are no Amazon males), it puts on evidence the participation of mate-choice copying in complex relationships between species sharing the same ecology – throughout its geographic

range, Amazons live always in sympatry with at least one of its parental species (Schlupp, Parzefall & Schartl, 2002). Mate-choice copying could, indeed, be contributing to the maintenance of this and other complex gynogenetic breeding systems. It also throws light to the donor males' behavioural paradox, since males were thought to derive no benefits from mating with heterospecific females (Schlupp *et al.*, 1994; Heubel *et al.*, 2008).

Additionally, this example also raises the question on whether mate-choice copying could facilitate or even be at the origin of such hybrid speciation events. This could be tested by studying the incidence of mate-choice copying in both the parental and hybrid species of known cases of hybridization, like the Amazon molly complex, but also others such as *Squalius alburnoides* (Cyprinidae fish) (Cunha *et al.*, 2011), *Heliconius* butterflies (Mavarez *et al.*, 2006), African cichlid fishes (Seehausen, 2004; Selz *et al.*, 2014) and Darwin finches (Grant & Grant, 2008). The single hybridization event giving rise to the Amazon molly occurred probably 100 000 years ago (Schlupp, 2005; Stöck *et al.*, 2010). Researchers have been trying to recreate the hybrid in the laboratory but with no success so far. Therefore, it will be extremely hard – not to say impossible – to determine the role of mate-choice copying in the origin of the Amazon molly. Nonetheless, heterospecific mate-choice copying experiments between the Amazon molly parental species have never been done. In these species, mate-choice copying is stronger in a conspecific context (Hill & Ryan, 2006; Heubel *et al.*, 2008), but it would be important to know how much of this dynamic can change in a heterospecific context. Such experiments would be extremely helpful to ascertain how many times mate-choice copying increases the frequency with which Atlantic molly females (the maternal species) mate with sailfin molly males (the paternal species) and, hence, how many opportunities mate-choice copying may have provided in the past for the hybrid formation of the Amazon molly. For *Heliconius* butterflies, hybrid phenotypes were successfully obtained

885 in the laboratory (Rieseberg *et al.*, 2003; Mavarez *et al.*, 2006), meaning that in this case
886 mate-choice copying experiments could even attempt to measure not only mating
887 preference but also the number of hybrid offspring that is produced with and without
888 copying.
889
890 **(3) When, between species in secondary contact, copied preferences reinforce or**
891 **preserve reproductive isolation**
892 If hybridization is unsuccessful – when premating barriers are incomplete but postmating
893 barriers are strong (Fig. 1) – the outcome will be very different from the above scenarios
894 (scenario 4c in Fig. 3). Hybrids will be less vigorous and could even be inviable or sterile
895 (Coyne & Orr, 2004). Therefore, the third possible consequence of mate-choice copying
896 as a promoter of hybridization is a significant reduction in the fitness of the copying
897 and/or copied individuals. Heterospecific mate-choice copying will become decreasingly
898 adaptive in this scenario, at least to one of the species involved, which in the short term
899 can even increase the risk of local extinction and be interpreted as a type of reproductive
900 interference.
901 Reproductive interference occurs when two species interfere with each other
902 during mating, either by participating in heterospecific matings or by hampering the other
903 species conspecific matings (Gröning & Hochkirch, 2008). This could have fitness
904 consequences to at least one of the species, leading to its competitive exclusion (Kishi,
905 Nishida & Tsubaki, 2009). Reproductive interference is caused by incomplete species
906 recognition and can occur in at least seven different ways: signal jamming, heterospecific
907 rivalry, misdirected courtship, heterospecific mating attempts, erroneous female choice,
908 heterospecific mating and hybridization (Gröning & Hochkirch, 2008). Mate-choice
909 copying, by inducing hybridization between species with incomplete recognition systems,

910 will be probably enhancing every one of these mechanisms. Copying could thus be
911 substantially interfering in the way species communicate, potentially handicapping one
912 or both species competitive abilities.

913 A case of misdirected courtship and heterospecific mating attempts is that
914 between introduced Trinidadian guppies (*Poecilia reticulata*) and the resident,
915 endangered, *Skiffia bilineata* species, another viviparous fish native from Central Mexico
916 (Valero, Garcia & Magurran, 2008). *S. bilineata* females, which are larger than guppy
917 females but morphologically resembling, probably represent a supernormal stimulus to
918 male guppies, who are attracted to large females (Herdman, Kelly & Godin, 2004). Since
919 both species cannot effectively hybridise as they are phylogenetically too distant –
920 guppies belong to the Poeciliidae family and *S. bilineata* to the Goodeidae family – male
921 guppies do not appear to derive benefits from courting heterospecific females. But
922 knowing that female guppies mate-choice copy, it is not impossible that male guppies
923 gain the advantage of becoming more attractive to conspecific females once courting and
924 mating with heterospecific females, in much the same way as male sailfin mollies become
925 more attractive to conspecific females by courting Amazon mollies (Schlupp *et al.*, 1994;
926 Heubel *et al.*, 2008). This would not be directly promoting hybridization, since the two
927 species do not produce viable hybrids, and guppy females, instead of *S. bilineata* females,
928 would be the copiers. Nonetheless, it suggests how mate-choice copying by guppy
929 females can interfere with the reproductive system of the other species. Besides, mate-
930 choice copying by *S. bilineata* females could also exist and is worth testing. Such
931 experiments could be done rather easily and if mate-choice copying is demonstrated, it
932 could be enhancing the reproductive interference effects over *S. bilineata*, which has
933 already gone extinct from 50% of its native distribution area (De La Vega-Salazar, Avila–
934 Luna & Macías–Garcia, 2003).

In the long term, it is predictable that reproductive interference via mate-choice copying will end up reinforcing the process of species recognition, facilitating further speciation. Reinforcement will occur either because, in the copying species, it favours the females that do not copy – selection against mate-choice copying –, or because, in the copying or copied species, it leads populations to local extinction. Alternatively, the behaviour of mate-choice copying may be preserved if selection pressures act directly on the recognition system itself. This could still reinforce reproductive barriers by preventing heterospecific mate-choice copying while preserving the females' ability for conspecific mate-choice copying.

This poses the question of how species recognition, or behavioural isolation in general, evolves. If females share information with each other, behavioural isolation should also involve the ability to identify as poor-quality information the cues and signals coming from heterospecific females. The mate-choice copying literature provides evidence that females evaluate whether other females are good models to copy or not (Dugatkin & Godin, 1993; Amlacher & Dugatkin, 2005; Hill & Ryan, 2006; Vukomanovic & Rodd, 2007; Waynforth, 2007; Yorzinski & Platt, 2010). Then, it is possible that species that do not perform heterospecific mate-choice copying are species where female-female recognition has successfully evolved as an additional reproductive barrier to gene flow.

In all three hybridization scenarios (4a to 4c in Fig. 3), the fate of the F1s and F2s is also very important. As we have seen, hybrids' fitness will determine whether hybridization is participating in reinforcing barriers to gene flow (if hybrids pay costs), or whether hybridization is generating new species, or recovering genetic variability (if there is some degree of hybrid viability) (Fig. 1). But there are other questions remaining. Will hybrids be more or less prone to copy? In which direction will they copy more often,

towards the maternal or the paternal species? The patterns of mate-choice behaviour of the hybrid generations will, therefore, be crucial to the role of mate-choice copying on long-term genetic introgression or adaptive radiation and hybrid speciation patterns that will follow, as well as to the ecological competences of the new lineages.

V. CONCLUSIONS

(1) Here we have described and reviewed mate-choice copying behaviour by females, and have detailed why it is considered an important mechanism of female mate choice. Furthermore, we outline how it can subsequently affect the course of sexual selection, by strengthening or weakening barriers to reproductive isolation. Such a conceptual framework was still lacking in the literature, and here we present a comprehensive theoretical basis for the role of mate-choice copying in both speciation and hybridization.

(2) Previous studies had already suggested the participation of mate-choice copying in the speciation process, but no specific evolutionary scenario has been proposed. Here, by merging mate-choice copying theory with speciation theory, we envisioned the ways by which this behaviour can truly affect speciation. By predicting in which scenarios mate-choice copying is more or less prone to facilitate or reinforce reproductive isolation, we can now study its occurrence and prevalence in a number of new species and ecological conditions. We particularly highlight the importance of environmental complexity and genotype-by-environment interactions, leading to fine-grained spatial variation and local adaptation, which are fundamental conditions for mate-choice copying to emerge as a driving force of speciation.

(3) Moreover, mate-choice copying may not only facilitate reproductive isolation setting the stage for speciation, but at the same time, and with less stringent conditions, it may also have the potential to direct sexual selection towards hybridization. Interesting, it is also by promoting or facilitating hybridization, that mate-choice copying could be increasing species' opportunities for adaptive introgression and radiation, hybrid speciation and reinforcement, which are hybridization outcomes that have been increasingly recognised to have potential major roles in speciation events.

(4) These new hypotheses challenge not only the view of the role of social learning in species evolution but also sheds light on the behavioural mechanisms that could be at the origin of speciation and hybridization, opening a new avenue of research for both theoretical and experimental studies.

VI. ACKNOWLEDGEMENTS

This study was financed by Portuguese National Funds, through FCT – Fundação para a Ciência e a Tecnologia, within the project UID/BIA/00329/2013 and through SAMV Post-Doctoral Research Grant (SFRH/BPD/66042/2009), and by the University of Oklahoma.

VII. REFERENCES:

ABBOTT, R., ALBACH, D., ANSELL, S., ARNTZEN, J. W., BAIRD, S. J. E., BIERNE, N., BOUGHMAN, J., BRELSFORD, A., BUERKLE, C. A., BUGGS, R., BUTLIN, R. K., DIECKMANN, U., EROUKHMANOFF, F., GRILL, A.,

1008 CAHAN, S. H., *et al.* (2013). Hybridization and speciation. *Journal of*
1009 *Evolutionary Biology* **26**, 229–246.
1010 AGRAWAL, A. F. (2001). The evolutionary consequences of mate copying on male
1011 traits. *Behavioural Ecology & Sociobiology* **51**, 33–40.
1012 ALONZO, S. H. (2008). Female mate choice copying affects sexual selection in wild
1013 populations of the ocellated wrasse. *Animal Behaviour* **75**, 1715–1723.
1014 AMLACHER, J. & DUGATKIN, L. A. (2005). Preference for older over younger models
1015 during mate-choice copying in young guppies. *Ethology Ecology & Evolution* **17**,
1016 161–169.
1017 ANDERSSON, M. & SIMMONS, L. W. (2006). Sexual selection and mate choice.
1018 *Trends in Ecology & Evolution* **21**, 296–302.
1019 ANDERSSON, M. (1994). *Sexual Selection*. Princeton University Press.
1020 ANDERSSON, M. (1982). Female choice selects for extreme tail length in a widowbird.
1021 *Nature* **299**, 818–820.
1022 APLIN, L. M., FARINE, D. R., MORAND-FERRON, J., COCKBURN, A.,
1023 THORNTON, A. & SHELDON, B. C. (2015). Experimentally induced
1024 innovations lead to persistent culture via conformity in wild birds. *Nature* **518**,
1025 538–543.
1026 ARNEGARD, M. E. & KONDRASHOV, A. S. (2004). Sympatric speciation by sexual
1027 selection alone is unlikely. *Evolution* **58**, 222–237.
1028 ARNOLD, M. L. & MARTIN, N. H. (2009). Adaptation by introgession. *Journal of*
1029 *Biology* **8**, 82.
1030 BATEMAN, A. J. (1948). Intrasexual selection in Drosophila. *Heredity* **2**, 349–368.

1031 BELTMAN, J. B., HACCOU, P. & TEN CATE, C. (2003). The impact of learning foster
1032 species' song on the evolution of specialist avian brood parasitism. *Behavioural*
1033 *Ecology* **14**, 917–923.
1034 BIKHCHANDANI, S., HIRSHLEIFER, D. & WELCH, I. (1992). A Theory of Fads,
1035 Fashion, Custom, and Cultural Change as Informational Cascades. *Journal of*
1036 *Political Economy* **100**(5), 992–1026.
1037 BIKHCHANDANI, S., HIRSHLEIFER, D. & WELCH, I. (1998). Learning from the
1038 behavior of others: conformity fads and informational cascades. *Journal of*
1039 *Economic Perspectives* **12**, 151–170.
1040 BOURNE, E. C., BOCEDI, G., TRAVIS, J. M. J., PAKEMAN, R. J., BROOKER, R. W.
1041 & SCHIFFERS, K. (2014). Between migration load and evolutionary rescue:
1042 dispersal, adaptation and the response of spatially structured populations to
1043 environmental change. *Proceedings of the Royal Society B: Biological Sciences*,
1044 **281**(1778), 20132795–20132795.
1045 BOURSOT, P., AUFFRAY, J.-C., BRITTON-DAVIDIAN, J. & BONHOMME, F.
1046 (1993). The evolution of house mice. *Annual Review of Ecology, Evolution, and*
1047 *Systematics* **24**, 119–152.
1048 BRADBURY, J. W. & GIBSON, R. M. (1983). Leks and mate choice. In P. P. G.
1049 Bateson, ed. *Mate choice*. Pages 109–138. Cambridge University Press,
1050 Cambridge.
1051 BRADBURY, J. W. (1981). The evolution of leks. In R. D. Alexander and D. W. Tinkle,
1052 eds. *Natural selection and social behaviour: recent research and new theory*.
1053 Pages 138–169. Lackwell, Oxford.

1054 BRENNAN, B. J., FLAXMAN, S. M. & ALONZO, S. H. (2008). Female alternative
1055 reproductive behaviors: The effect of female group size on mate assessment and
1056 copying. *Journal of Theoretical Biology* **253**, 561–569.
1057 BRIGGS, S. E., GODIN, J.-G. J. & DUGATKIN, L. A. (1996). Mate-choice copying
1058 under predation risk in the Trinidadian guppy (*Poecilia reticulata*). *Behavioral*
1059 *Ecology* **7**, 151–157.
1060 BROOKS, R. (1998). The importance of mate copying and cultural inheritance of mating
1061 preferences. *Trends in Ecology & Evolution* **13**, 45–46.
1062 BUERKLE, C. A., WOLF, D. E. & RIESEBERG, L. H. (2003). The origin and extinction
1063 of species through hybridization. In C. A. Brigham, and M. W. Schwartz, eds.
1064 *Population Viability in Plants: Conservation, Management, and Modelling of*
1065 *Rare Plants*. Pp. 117–141. Springer Verlag, Heidelberg.
1066 BURDFIELD-STEEL, E. R. & SHUKER, D.M. (2011). Reproductive interference.
1067 *Current Biology* **21**, 450–451.
1068 BUTLIN, R. & THE MARIE CURIE SPECIATION NETWORK. (2012). What do we
1069 need to know about speciation? *Trends in Ecology & Evolution* **27**(1), 27–39.
1070 BUTLIN, R. K., BRIDLE, J. R. & SCHLUTER, D. (2008). Speciation and patterns of
1071 Biodiversity. In *Speciation and Patterns of Biodiversity*. Ecological Reviews.
1072 Edited by Butlin, R. K., Bridle, J. R and Schluter, D. Series Editor Jones, H. Pp
1073 1–14. Cambridge University Press.
1074 CANALE, C. I. & HENRY, P.-Y. (2010). Adaptive phenotypic plasticity and resilience
1075 of vertebrates to increasing climatic unpredictability. *Climate Research* **43**, 135–
1076 147.
1077 CARLSON, S. M., CUNNINGHAM, C. J. & WESTLEY, P.A. H. (2014). Evolutionary
1078 rescue in a changing world. *Trends in Ecology and Evolution* **29**(9), 521–530.

1079 CORNWALLIS, C. K. & ULLER, T. (2010). Towards an evolutionary ecology of sexual
1080 traits. *Trends in Ecology & Evolution* **25**, 145–52.
1081 COYNE, J. A. & ORR, H. A. (2004). *Speciation*. Sinauer Associates, Inc. Sunderland,
1082 Massachusetts, USA.
1083 CUNHA, C., DOADRIO, I., ABRANTES, J. & COELHO, M. M. (2011). The
1084 evolutionary history of the allopolyploid *Squalius alburnoides* (Cyprinidae)
1085 complex in the northern Iberian Peninsula. *Heredity* **106**, 100–112.
1086 DANCHIN, É. & WAGNER, R. H. (2008). Cultural Evolution. In *Behavioural Ecology*,
1087 eds. Danchin É, Giraldeau L.-A. & Cézilly F. Pp. 693–726. Oxford University
1088 Press, Oxford.
1089 DANCHIN, É., GIRALDEAU, L.-A. & WAGNER, R. H. (2008). An Information-Driven
1090 Approach to Behaviour. In *Behavioural Ecology*, eds. Danchin É, Giraldeau L.-
1091 A. & Cézilly F. Pp. 97–129. Oxford University Press, Oxford.
1092 DANCHIN, É., CHARMANTIER, A., CHAMPAGNE, F. A., MESOUDI, A., PUJOL,
1093 B. & BLANCHET, S. (2011). Beyond DNA: integrating inclusive inheritance into
1094 an extended theory of evolution. *Nature Reviews Genetics* **12**, 475–486.
1095 DANCHIN, É., GIRALDEAU, L.-A., VALONE, T. J. & WAGNER, R. H. (2004). Public
1096 information: from nosy neighbors to cultural evolution. *Science* **305**, pp. 487–491.
1097 DANCHIN, É. & WAGNER, R. (2010). Inclusive heritability: combining genetic and
1098 non-genetic information to study animal behavior and culture. *Oikos* **119**, 210–
1099 218.
1100 DANCHIN, É. (2013). Avatars of information: towards an inclusive evolutionary
1101 synthesis. *Trends in Ecology & Evolution* **28**(6), 351–358.
1102 DARWIN, C. (1859). *On the Origin of Species*. John Murray, London.

1103 DARWIN, C. (1871). *The Descent of Man*, *and Selection in Relation to Sex*. John Murray,
1104 London.
1105 DE LA VEGA-SALAZAR, M. Y., AVILA-LUNA, E. & MACÍAS-GARCIA, C. (2003).
1106 Ecological evaluation of local extinction: the case of two genera of endemic
1107 Mexican fish. *Zoogoneticus* and *Skiffia*. *Biodiversity and Conservation* **12**, 2043–
1108 2056.
1109 DELBARCO-TRILLO, J. & JOHNSTON, R. (2010). Adult female hamsters require long
1110 and sustained exposures to heterospecific males to avoid interspecific mating.
1111 *Evolutionary Ecology* **25**, 391–401.
1112 DRULLION, D. & DUBOIS, F. (2008). Mate-choice copying by female zebra finches,
1113 Taeniopygia guttata: what happens when model females provide inconsistent
1114 information? *Behavioral Ecology and Sociobiology* **63**, 269–276.
1115 DUCKWORTH, R. A. (2009). The role of behavior in evolution: a search for mechanism.
1116 *Evolutionary Ecology* **23**, 513–531.
1117 DUGATKIN, L. A (1996*a*). Copying and mate choice. In: *Social Learning in Animals:*
1118 *the Roots of Culture*, eds. Heyes C. M. & Galef B. G. Jr. Pp. 85–106. Academic
1119 Press, San Diego.
1120 DUGATKIN, L. A. & GODIN, J. G. J. (1992). Reversal of female mate choice by copying
1121 in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society of London*
1122 *Series B–Biological Sciences* **249**, 179–184.
1123 DUGATKIN, L. A. & GODIN, J. G. J. (1993). Female mate copying in the guppy
1124 (*Poecilia reticulata*) – age-dependent effects. *Behavioral Ecology* **4**, 289–292.
1125 DUGATKIN, L. A. (1992). Sexual selection and imitation-females copy the mate choice
1126 of others. *The American Naturalist* **139**, 1384–1389.

DUGATKIN, L. A. (1996*b*). Interface between culturally based preferences and genetic preferences: female mate choice in *Poecilia reticulate*. *Proceedings of the National Academy of Sciences of the USA* **93**, 2770–2773.

DUGATKIN, L. A. (2005). Mistakes and the evolution of copying. *Ethology Ecology and Evolution* **17**, 327–333.

DUGATKIN, L. A. & GODIN, J.-G. J. (1998). Effects of hunger on mate-choice copying in the guppy. *Ethology* **104**, 194–202.

DUGATKIN, L. A. & HÖGLUND, J. (1995). Delayed breeding and the evolution of mate copying in lekking species. *Journal of Theoretical Biology* **174**, 261–267.

DUKAS, R. (2013). Effects of learning on evolution: robustness, innovation and speciation. *Animal Behaviour* **85**, 1023–1030.

ENDLER, J. A. (1983). Natural and sexual selection on color patterns in Poeciliid fishes. *Environmental Biology of Fishes* **9**, 173–190.

FELSENSTEIN, J. (1981). Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution* **35**, 124–138.

FILCHAK, K. E., ROETHELE, J. B. & FEDER, J. L. (2000). Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. *Nature* **407**, 739–742.

FISHER, R. A. (1930). *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.

FOWLER-FINN, K. D., SULLIVAN-BECKERS, L., RUNCK, A. M., HEBETS, E. A. (2015). The complexities of female mate choice and male polymorphisms: Elucidating the role of genetics, age, and mate-choice copying. *Current Zoology* **61**, 1015–1035.

1151 FUTUYMA, D. J. & MAYER, G. C. (1980). Non-allopatric speciation in animals.
1152 **Systematic Zoology 29**(3), 254–271.
1153 GALEF, B. G JR. & WHITE, D. J. (1998). Mate-choice copying in japanese quail,
1154 *Coturnix coturnix japonica*. *Animal Behaviour* **55**, 545–552.
1155 GALE,F B. G JR. & WHITE, D. J. (2000). Evidence of social effects on mate choice in
1156 vertebrates. *Behavioural Processes* **51**, 167–175.
1157 GIBSON, R. M. & HÖGLUND, J. (1992). Copying and sexual selection. *Trends in*
1158 *Ecology & Evolution* **7**, 229–232.
1159 GIRALDEAU, L.-A., VALONE, T. J. & TEMPLETON, J. J. (2002). Potential
1160 disadvantages of using socially-acquired information. *Philosophical Transactions*
1161 *of the Royal Society of London Series B-Biological Sciences* **357**, 1559–1566.
1162 GODIN, J. G. J. & HAIR, K. P. E. (2009). Mate-choice copying in free-ranging
1163 Trinidadian guppies (*Poecilia reticulata*). *Behaviour* **146**(10), 1443–1461.
1164 GODIN, J. G. J., HERDMAN, E. J. E. & DUGATKIN, L. A. (2005). Social influences
1165 on female mate choice in the guppy, *Poecilia reticulata*: generalized and
1166 repeatable trait-copying behaviour. *Animal Behaviour* **69**, 999–1005.
1167 GOSDEN, T. P., SVENSSON, E. I. (2008). Spatial and temporal dynamics in a sexual
1168 selection mosaic. *Evolution* **62**, 845–56.
1169 GRANT, B. R. & GRANT, P. R. (2008). Fission and fusion of Darwin's finches
1170 populations. *Philosophical transactions of the Royal Society of London*. *Series B*,
1171 *Biological sciences* **363**, 2821–9.
1172 GRANT, B. R. & GRANT, P. R. (1996). Cultural Inheritance of Song and Its Role in the
1173 Evolution of Darwin's Finches. *Evolution* **50**(6), 2471–2487.
1174 GRANT, P. R. & GRANT, B. R. (1994). Phenotypic and genetice effects of hybridization
1175 in Darwin's finches. *Evolution* **48**, 297–316.

GRANT, P. R. & GRANT, B. R. (2009). The secondary contact phase of allopatric speciation in Darwin's finches. *Proceedings of the National Academy of Science of the United States of America* **106**, 20141–20148.

GRANT, P. R. & GRANT, B. R. (1997). Hybridization, sexual imprinting, and mate choice. *The American Naturalist* **149**, 1–28.

GRÖNING, J. & HOCHKIRCH, A. (2008). Reproductive interference between animal species *The Quarterly Review of Biology* **83**, 257–282.

HARRISON, S. J., THOMSON, I. R., GRANT, C. M. & BERTRAM, S. M. (2013). Calling, courtship, and condition in the fall field cricket, *Gryllus pennsylvanicus*. *PLoS ONE* **8(3)**, e60356.

HERDMAN, E. J. E., KELLY, C. D. & GODIN, J. G. J. (2004). Male mate choice in the guppy (*Poecilia reticulata*). do males prefer larger females as mates? *Ethology* **110**, 97–111.

HEUBEL, K. U., HORNHARDT, K., OLLMANN, T., PARZEFALL, J., RYAN, M. J. & SCHLUPP, I. (2008). Geographic variation in female mate-copying in the species complex of a unisexual fish, Poecilia Formosa. *Behaviour* **145**, 1041–1064.

HILL, S. E. & RYAN, M. J. (2006). The role of model female quality in the mate choice copying behaviour of sailfin mollies. *Biology Letters* **2**, 203–205.

HÖGLUND, J., ALATALO, R. V., GIBSON, R. M. & LUNBERG, A. (1995). Mate-choice copying in black grouse. *Animal Behaviour* **49**, 1627–1633.

HOUDE, A. E. (1987). Mate choice based upon naturally occurring color-pattern variation in a guppy population. *Evolution* **41**, 1–10.

HOUDE, A. E. (1988). Genetic difference in female choice between two guppy populations. *Animal Behaviour* **36**, 510–516.

1201 HOUDE, A. E. & ENDLER, J. A. (1990). Correlated evolution of female mating
1202 preference and male color patterns in the guppy Poecilia reticulata. *Science* **248**:
1203 1405–1408.
1204 IMMELMAN, K. (1975). Ecological significance of imprinting and early learning.
1205 *Annual Review of Ecology, Evolution, and Systematics* **6**, 15–37.
1206 INGLEBY, F. C., HUNT, J. & HOSKEN, D. J. (2010). The role of genotype-by-
1207 environment interactions in sexual selection. *Journal of Evolutionary Biology* **23**,
1208 2031–45.
1209 IRWIN, D. E. & PRICE, T. (1999). Sexual imprinting, learning and speciation. *Heredity*
1210 **82**, 347–354.
1211 JABLONKA, E., LAMB, M. J. & AVITAL, E. (1998). 'Lamarckian' mechanisms in
1212 Darwinian evolution. *Trends in Ecology & Evolution* **13**, 206–210.
1213 JOHNSON, W. E., ONORATO, D. P., ROELKE, M. E., LAND, E. D., CUNNINGHAM,
1214 M., BELDEN, R. C., MCBRIDE, R., JANSEN, D., LOTZ, M., SHINDLE, D.,
1215 HOWARD, J., WILDT, D. E., PENFOLD, L. M., HOSTETLER, J. A., OLI, M.
1216 K., O'BRIEN, S. J. (2010). Genetic restoration of the Florida panther. *Science*
1217 **329**, 1641–1645.
1218 KANG, J. H., SCHARTL, M., WALTER, R. B. & MEYER, A. (2013). Comprehensive
1219 phylogenetic analysis of all species of swordtails and platies (Pisces: Genus
1220 *Xiphophorus*). uncovers a hybrid origin of a swordtail fish, *Xiphophorus*
1221 *monticolus*, and demonstrates that the sexually selected sword originated in the
1222 ancestral lineage of the genus, but was lost again secondarily. *BMC Evolutionary*
1223 *Biology* 13, 25.
1224 KAVALIERS, M., CHOLERIS, E., AGMO, A., BRAUN, W. J., COLWELL, D. D.,
1225 MUGLIA, L. J., OGAWA, S. & PFAFF, D. W. (2006). Inadvertent social

1226 information and the avoidance of parasitized male mice: a role for oxytocin.
1227 *Proceedings of the National Academy of Sciences of the USA* **103**, 4293–4298.
1228 KENDAL, R. L., COOLEN, I., VAN BERGEN, Y. & LALAND, K. L. (2005). Trade-
1229 Offs in the Adaptive Use of Social and Asocial Learning. *Advances in the Study*
1230 *of Behavior*. Academic Press, Volume 35, Pages 333-379.
1231 KIM, S. C. & RIESEBERG, L. H. (1999). Genetic architecture of species differences in
1232 annual sunflowers: implications for adaptive trait introgression. *Genetics* **153**,
1233 965–977.
1234 KIRKPATRICK, M. & DUGATKIN, L. A. (1994). Sexual selection and the evolutionary
1235 effects of copying mate choice. *Behavioral Ecology & Sociobiology* **34**, 443–449.
1236 KIRKPATRICK, M. (1982). Sexual selection and the evolution of female choice.
1237 *Evolution* **36**, 1–12.
1238 KISHI, S., NISHIDA, T. & TSUBAKI, Y. (2009). Reproductive interference determines
1239 persistence and exclusion in species interactions. *Journal of Animal Ecology* **78**,
1240 1043–1049.
1241 KOKKO, H. (1997). Evolutionarily stable strategies of age-dependent sexual
1242 advertisement. *Behavioral Ecology and Sociobiology* **41**, 99–107.
1243 KOKKO, H. & BROOKS, R. (2003). Sexy to die for? Sexual selection and the risk of
1244 extinction. *Annales Zoologici Fennici* **40**, 207–219.
1245 KRAAIJEVELD, K., KRAAIJEVELD-SMIT, F. J. L. & MAAN, M. E. (2011). Sexual
1246 selection and speciation: the comparative evidence revisited. *Biological Reviews*
1247 **86**, 367–377.
1248 KUNTE, K., SHEA, C., AARDEMA, M. L., SCRIBER, J. M., JUENGER, T. E.,
1249 GILBERT, L. E. & KRONFORST, M. R. (2011). Sex chromosome mosaicism

and hybrid speciation among tiger swallowtail butterflies. *PLoS Genetic* **7**, e1002274.

LALAND, K. N., ULLER, T., FELDMAN, M. W., STERELNY, K., MÜLLER, G. B., MOCZEK, A., JABLONKA, E. & ODLING-SMEE, J. (2015). The extended evolutionary synthesis: its structure, assumptions and predictions. *Proceedings of the Royal Society of London Series B-Biological Sciences* **282**, (2015)1019.

LALAND, K. N. (1994a). Sexual selection with a culturally transmitted mating preference. *Theoretical Population Biology* **45**, 1–15.

LALAND, K. N. (1994b). On the evolutionary consequences of sexual imprinting. *Evolution* **48**, 477–489.

LANDE, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the USA* **78**, 3721–3725.

LEADBEATER, E. (2009). Social learning: what do Drosophila have to offer? *Current Biology* **19**, R378–R380.

LINDHOLM, M. (2015). DNA Dispose, but Subjects Decide. Learning and the Extended Synthesis. *Biosemiotics* **8**(3), 443–461.

LORENZ, K. (1935). Der Kumpan in der Umwelt des Vogels. *Journal of Ornithology* **83**, 137–213.

LOSEY, G. S., JR., STANTON, F. G., TELECKY, T. M., TYLER III, W. A. & ZOOLOGY 691 GRADUATE SEMINAR CLASS. (1986). Copying others, an evolutionarily stable strategy for mate choice: a model. *The American Naturalist* **128**, 653–664.

LUMLEY, A. J., MICHALCZYK, L., KITSON, J. J. N., SPURGIN, L. G., MORRISON, C. A., GODWIN, J. L., DICKINSON, M. E., MARTIN, O. Y., EMERSON, B.

1274 C., CHAPMAN, T. & GAGE, M. J. G. (2015). Sexual selection protects against
1275 extinction. *Nature* **522**, 470–473.
1276 MAJERUS, M. E. N, O'DONALD, P., KEARNS, P. W. E. & IRELAND, H. (1986).
1277 Genetics and evolution of female choice. *Nature* **321**(6066), 164–167.
1278 MAJERUS, M. E. N. (1986). The genetics and evolution of female choice. *Trends in*
1279 *Ecology & Evolution* **1**, 1–7.
1280 MALLET, J. (2005). Hybridization as an invasion of the genome. *Trends in Ecology and*
1281 *Evolution* **20**(5), 229–237.
1282 MALLET, J. (2007). Hybrid speciation. *Nature* **446**, 279–283
1283 MAVAREZ, J., SALAZAR, C. A., BERMINGHAM, E., SALCEDO, C., JIGGINS, D.
1284 C. & LINAREZ, M. (2006). Speciation by hybridization in Heliconius butterflies.
1285 *Nature* **441**, 868–871.
1286 MAYR, E. (1963). *Animal species and evolution*. Harvard University Press, Cambridge,
1287 Massachusetts, xvi + 797 pp.
1288 MEAD, L. S. & ARNOLD, S. J. (2004). Quantitative genetic models of sexual selection.
1289 *Trends in Ecology & Evolution* **19**, 264–271.
1290 MENDELSON, T. C., SHAW, K. L. (2012). The (mis)concept of species recognition.
1291 *Trends in Ecology & Evolution* **27**, 421–427.
1292 MERY, F., VARELA, S. A. M., DANCHIN, É., BLANCHET, S., PAREJO, D.,
1293 COOLEN, I., WAGNER, R. H. (2009). Public Versus Personal Information for
1294 Mate Copying in an Invertebrate. *Current Biology* **19**(9), 730–734.
1295 MILLER, C. W. & SVENSSON, E. I. (2014). Sexual Selection in Complex
1296 Environments. *Annual Review of Entomology* **59**, 427–45.
1297 MINA, M. V., MIRONOVSKY, A. N. & DGEBUADZE, Y. Y. (1996). Lake Tana large
1298 barbs: phenetics, growth and diversification. *Journal of Fish Biology* **48**, 383–404.

1299 MOEN, R. A., PASTOR, J. & COHEN, Y. (1999). Antler growth and extinction of Irish
1300 elk. *Evolutionary Ecology Research* **1**, 235–249.
1301 MØLLER, A. P. (1994). *Sexual Selection and the Barn Swallow*. Oxford University
1302 Press, Oxford.
1303 NOLTE, A. W. & TAUTZ, D. (2010). Understanding the onset of hybrid speciation.
1304 *Trends in Genetics* **26**, 54–8.
1305 NORDELL, S. E. & VALONE, T. J. (1998). Mate choice copying as public information.
1306 *Ecology Letters* **1**, 74–76.
1307 NOSIL, P. (2012). *Ecological Speciation*. Oxford Series in Ecology and Evolution.
1308 Edited by Harvey, P. H., May, R. M., Godfray, C. J. & Dunne, J. A. Oxford
1309 University Press. Oxford, New York.
1310 NOSIL, P., VINES, T. H. & FUNK, D. J. (2005). Reproductive isolation caused by
1311 natural selection against immigrants from divergent habitats. *Evolution* **59**(4),
1312 705–719.
1313 OWENS, I. P. F., ROWE, C. & THOMAS, A. L. R. (1999). Sexual selection, speciation
1314 and imprinting: separating the sheep from the goats. *Trends in Ecology &*
1315 *Evolution* **14**, 131–132.
1316 PAYNE, R. B., PAYNE, L. L., WOODS, J. L. & SORENSON, M.D. (2000). Imprinting
1317 and the origin of parasite-host species associations in brood-parasitic indigobirds,
1318 Vidua chalybeata. *Animal Behaviour* **59**, 69–81.
1319 PAYNE, R. B., PAYNE, L. L. & WOODS, J. L. (1998). Song learning in brood parasitic
1320 indigobirds *Vidua chalybeata*: song mimicry of the host species. *Animal*
1321 *Behaviour* **55**, 1537–1553.
1322 PFENNING, K. S. (2007). Facultative Mate Choice Drives Adaptive Hybridization.
1323 *Science* **318**, 965–967.

1324 POMIANKOWSKI, A. (1987). The costs of choice in sexual selection. *Journal of*
1325 *Theoretical Biology* **128**, 195–218.
1326 PRICE, T. D., QVARNSTROM, A. & IRWIN, D. E. (2003). The role of phenotypic
1327 plasticity in driving genetic evolution. *Proceedings of the Royal Society of London*
1328 *Series B-Biological Sciences* **270**, 1433–1440.
1329 PROMISLOW, D. E. L., MONTGOMERIE, R. & MARTIN, T. E. (1992). Mortality
1330 costs of sexual dimorphism in birds. *Proceedings of the Royal Society of London*
1331 *Series B-Biological Sciences* **250**, 143–150.
1332 PRUETT-JONES, S. (1992). Independent versus nonindependent mate choice: do
1333 females copy each other? *The American Naturalist* **140**, 1000–1009.
1334 REYER, H.-U. (2008). Mating with the wrong species can be right. *Trends in Ecology*
1335 *and Evolution* **23**, 289–292.
1336 REYNOLDS, J. D. & GROSS, M. R. (1990). Costs and benefits of female mate choice:
1337 Is there a lek paradox? *The American Naturalist* **136**, 230–243.
1338 RIESEBERG, L. H., RAYMOND, O., ROSENTHAL, D. M., LAI, Z., LIVING-STONE,
1339 K., NAKAZATO, T., DURPHY, J. L., SCHWARZBACH, A. E., DONOVAN,
1340 L. A. & LEXER, C. (2003). Major ecological transitions in wild sunflowers
1341 facilitated by hybridization. *Science* **301**, 1211–1216.
1342 RIEUCAU, G. & GIRALDEAU, L.-A. (2011). Exploring the costs and benefits of social
1343 information use: an appraisal of current experimental evidence. *Philosophical*
1344 *transactions of the Royal Society of London. Series B, Biological sciences* **366**,
1345 949–957.
1346 ROSENTHAL, G. G. & GARCIA DE LEON, F. J. (2006). Sexual behavior, genes, and
1347 evolution in *Xiphophorus*. *Zebrafish* **3**, 85–90.

1348 RUNDLE, H. D. & NOSIL, P. (2005). Ecological speciation. *Ecology Letters* **8**, 336–
1349 352.
1350 RYAN, M. J. & WAGNER, W. E. JR. (1987). Asymmetries in Mating Preferences
1351 between Species: Female Swordtails Prefer Heterospecific Males. *Science*
1352 **236**(4801), 595–597.
1353 RYAN, M. J., AKRE, K. L. & KIRKPATRICK, M. (2007). Mate choice. *Current Biology*
1354 **17**, R313–R316.
1355 SALAZAR, C., BAXTER, S. W., PARDO-DIAZ, C., WU, G., SURRIDGE, A.,
1356 LINARES, M., BERMINGHAM, E., & JIGGINS, C. D. (2010). Genetic
1357 Evidence for Hybrid Trait Speciation in Heliconius Butterflies. *PLoS Genetics*
1358 **6**(4), e1000930.
1359 SANTOS, M., MATOS, M. & VARELA, S. A. M. (2014). Negative public information
1360 in mate-choice copying helps the spread of a novel trait. *The American Naturalist*
1361 **184**(5), 658–672.
1362 SCHLIEWEN, U. K., DIETHARD, T. & PÄÄBO, S. (1994). Sympatric speciation
1363 suggested by monophyly of crater lake cichlids. *Nature* **368**, 629–632.
1364 SCHLUPP, I. & RYAN, M. J. (1996). Mixed-species shoals and the maintenance of a
1365 sexual-asexual mating system in mollies. *Animal Behaviour* **52**, 885–890.
1366 SCHLUPP, I. (2005). The evolutionary ecology of gynogenesis. *Annual Review of*
1367 *Ecology Evolution and Systematics* **36**, 399–417.
1368 SCHLUPP, I., MARLER, C. & RYAN, M. J. (1994). Benefit to male sailfin mollies of
1369 mating with heterospecific females. *Science* **263**, 373–374.
1370 SCHLUPP, I., PARZEFALL, J. & SCHARTL, M. (2002). Biogeography of the Amazon
1371 molly, *Poecilia formosa*. *Journal of Biogeography* **29**, 1–6.

1372 SCOTT-PHILLIPS, T. C., LALAND, K. N., SHUKER, D. M., DICKINS, T. E. &
1373 WEST, S. A. (2013). The niche construction perspective. A critical appraisal.
1374 *Evolution* **68**, 1231–1243.
1375 SEEHAUSEN, O. (2004). Hybridization and adaptive radiation. *Trends in Ecology &*
1376 *Evolution* **19**, 198–207.
1377 SEEHAUSEN, O. (2013). Conditions when hybridization might predispose populations
1378 for adaptive radiation. *Journal of Evolutionary Biology* **26**, 279–281.
1379 SELZ, O. M., THOMMEN, R., MAAN, M. E. & SEEHAUSEN, O. (2014). Behavioural
1380 isolation may facilitate homoploid hybrid speciation in cichlid fish. *Journal of*
1381 *Evolutionary Biology* **27**, 275–289.
1382 SERVEDIO, M. R. & KIRKPATRICK, M. (1996). The evolution of mate choice copying
1383 by indirect selection. *The American Naturalist* **148**, 848–867.
1384 SERVEDIO, M. R. & DUKAS, R. (2013). Effects on population divergence of within-
1385 generational learning about prospective mates. *Evolution* **67**(8), 2363–2375.
1386 SERVEDIO, M. R., SÆTHER, S. A. & SÆTRE, G.-P. (2009). Reinforcement and
1387 learning. *Evolutionary Ecology* **23**, 109–123.
1388 SIROT, E. (2001). Mate-choice copying by females: the advantages of a prudent strategy.
1389 *Journal of Evolutionary Biology* **14**, 418–423.
1390 SMOLLA, M., ALEM, S., CHITTKA, L. & SHULTZ, S. (2016). Copy-when-uncertain:
1391 bumblebees rely on social information when rewards are highly variable. *Biololy*
1392 *Letters* **12**, (2016)0188.
1393 STAUBACH, F., LORENC, A., MESSER, P.W., TANG, K., PETROV, D. A. & TAUTZ
1394 D. (2012). Genome patterns of selection and introgression of haplotypes in natural
1395 populations of the house mouse (*Mus musculus*). *PLOS Genetics* **8**(8): e1002891.

1396 STEARNS, S. C. (1992). *The evolution of life histories*. Oxford University Press, New
1397 York.
1398 STÖCK, M., LAMPERT, K. P, MÖLLER, D., SCHLUPP, I. & SCHARTL, M. (2010).
1399 Monophyletic origin of multiple clonal lineages in an asexual fish (*Poecilia*
1400 *formosa*). *Molecular Ecology* **19**(23), 5204–5215.
1401 STÖHR, S. (1998). Evolution of mate choice copying: a dynamic model. *Animal*
1402 *Behaviour* **55**, 893–903.
1403 STREELMAN, J. T., & DANLEY, P. D. (2003). The stages of vertebrateevolutionary
1404 radiation. *Trends in Ecology & Evolution* **18**, 126–131.
1405 SWADDLE, J. P., CATHEY, M. G., CORRELL, M. & HODKINSON, B. P. (2005).
1406 Socially transmitted mate preferences in a monogamous bird: a non-genetic
1407 mechanism of sexual selection. *Proceedings of the Royal Society of London Series*
1408 *B-Biological Sciences* **272**, 1053–1058.
1409 TANAKA, Y. (1996). Sexual selection enhances population extinction in a changing
1410 environment. *Journal of Theoretical Biology* **180**, 197–206.
1411 TAYLOR, E. B., & BENTZEN, P. (1993). Evidence for multiple origins and sympatric
1412 divergence of trophic ecotypes of smelt (*Osmerus*) in northeastern North America.
1413 *Evolution* **47**, 813–832.
1414 TEN CATE, C. & VOS, D. R. (1999). Sexual imprinting and evolutionary processes in
1415 birds: a re-assessment. *Advances in the Study of Animal Behaviour* **28**, 1–31.
1416 TEN CATE, C. (2000). How learning mechanisms might affect evolutionary processes.
1417 *Trends in Ecology & Evolution* **15**(5), 179–181.
1418 TODESCO, M., PASCUAL, M. A., OWENS, G. L., OSTEVIK, K. L., MOYERS, B. T.,
1419 HÜBNER, S., HEREDIA, S. H., HAHN, M. A., CASEYS, C., BOCK, D. G. &

RIESEBERG, L. H. (2016). Hybridization and extinction. *Evolutionary Applications* **9**, 892–908.

UEHARA, T., YOKOMIZO, H. & IWASA, Y. (2005). Mate choice copying as Bayesian decision making. *The American Naturalist* **165**, 403–410.

VAKIRTZIS, A. (2011). Mate choice copying and nonindependent mate choice: a critical review. *Annales Zoologici Fennici* **48**, 91–107.

VALERO, A., GARCIA, C. M. & MAGURRAN, A. E. (2008). Heterospecific harassment of native endangered fishes by invasive guppies in Mexico. *Biology Letters* **4**, 149–152.

VALONE, T. J. & TEMPLETON, J. J. (2002). Public information for the assessment of quality: a widespread social phenomenon. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **357**, 1549–57.

VERZIJDEN, M. N., TEN CATE, C., SERVEDIO, M. R., KOZAK, G. M., BOUGHMAN, J. W. & SVENSSON, E. I. (2012). The impact of learning on sexual selection and speciation. *Trends in Ecology & Evolution* **27**(9), 511–519.

VERZIJDEN, M. N. & TEN CATE, C. (2007). Early learning influences species assortative mating preferences in Lake Victoria cichlid fish. *Biology Letters* **3**, 134–136.

VERZIJDEN, M. N., LACHLAN, R. F. & SERVEDIO, M. R. (2005). Female mate-choice behavior and sympatric speciation. *Evolution* **59**, 2097–2108.

VIA, S. (2001). Sympatric speciation in animals: the ugly duckling grows up. *Trends in Ecology & Evolution* **16**, 381–390.

VUKOMANOVIC, J. & RODD, F. H. (2007). Size-dependent female mate copying in the guppy (*Poecilia reticulata*). Large females are role models but small ones are not. *Ethology* **113**, 579–586.

1445 WADE, M. & PRUETT–JONES, S. (1990). Female copying increases the variance in
1446 male mating success. *Proceedings of the National Academy of Sciences of the USA*
1447 **87**, 5749–5753.
1448 WAGNER, R. H. & DANCHIN, É. (2010). A taxonomy of biological information. *Oikos*
1449 **119**, 203–209.
1450 WAYNFORTH, D. (2007). Mate choice copying in humans. Human *Nature* **18**, 264–
1451 271.
1452 WEISSING, F. J., EDELAAR, P. & VAN DOORN, G. S. (2011). Adaptive speciation
1453 theory: a conceptual review. *Behavioral Ecology and Sociobiology* **65**, 461–480.
1454 WESTNEAT, D. F., WALTERS, A., MCCARTHY, T. M., HATCH, M. I. & HEIN, W.
1455 K. (2000). Alternative mechanisms of nonindependent mate choice. *Animal*
1456 *Behaviour* **59**, 467–476.
1457 WHITE, D. J. & GALEF, B. G. (2000). "Culture" in quail: social influences on mate
1458 choices of female Coturnix japonica. *Animal Behaviour* **59**, 975–979.
1459 WHITNEY, K. D., RANDELL, R. A. & RIESEBERG, L. H. (2010). Adaptive
1460 introgression of abiotic tolerance traits in the sunflower *Helianthus annuus*. *New*
1461 *Phytologist* **187**, 230–239.
1462 WITTE, K. & NOLTEMEIER, B. (2002). The role of information in mate-choice copying
1463 in female sailfin mollies (*Poecilia latipinna*). *Behavioral Ecology and*
1464 *Sociobiology* **52**, 194–202.
1465 WITTE, K. & RYAN, M. J. (2002). Mate choice copying in the sailfin molly, *Poecilia*
1466 *latipinna*, in the wild. *Animal Behaviour* **63**, 943–949.
1467 WITTE, K. & RYAN, M. J. (1998). Male body length influences mate-choice copying in
1468 the sailfin molly *Poecilia latipinna*. *Behavioral Ecology* **9**, 534–539.

WITTE, K. & UEDING, K. (2003). Sailfin molly females (Poecilia latipinna). copy the rejection of a male. *Behavioral Ecology* **14**, 389–395.

WITTE, K., KNIEL, N. & KURECK, I. M. (2015). Mate-choice copying: Status quo and where to go. *Current Zoology* **61** (6), 1073–1081.

WOOD, C. C. & C. J. FOOTE. (1996). Evidence for sympatric geneticdivergence of anadromous and nonanadromous morphs of sock-eye salmon (*Oncorhynchus nerka*). *Evolution* **50**, 1265–1279.

YORZINSKI, J. L. & PLATT, M. L. (2010). Same-sex gaze attraction influences mate-choice copying in humans. *PLoS One* **5**, e9115.

ZINCK, L. & LIMA, S. Q. (2013). Mate Choice in *Mus musculus* Is Relative and Dependent on the Estrous State. *PLoS One* **8**, e66064.

FIGURE LEGENDS:

Fig. 1. Locating Mate-Choice Copying (MCC) in the classical framework of speciation and hybridization theories. Mate-choice copying is a form of social information, used for mate selection. Individuals acquire information about the quality of prospective mates by observing the mating experiences of other model individuals. Different individuals may copy different information and could learn from conspecifics or heterospecifics, which could help facilitating/reinforcing/preventing or promoting speciation and hybridization, respectively.

Fig. 2. The different mate-choice copying rules and their effects for reproductive isolation in sympatry. With any of the copying rules, mate-choice copying will not promote reproductive isolation between individuals of a population with different learned mate preferences. Mate-choice copying will always lead to convergent mate preferences and directional selection, instead of promoting reproductive isolation and species' fission.

Fig. 3. The six scenarios by which Mate-Choice Copying (MCC) may facilitate/reinforce/prevent or promote speciation and hybridization, respectively. When exchanging information with conspecifics, an individual's copied preferences may diverge or agree with the preferences learned by other individuals. Mate-choice copying may thus: facilitate (scenario 1); reinforce (scenario 2); or prevent (scenario 3) speciation. By contrast, when exchanging information with heterospecifics via convergent mate preferences (scenario 4), mate-choice copying may promote hybridization, with outcomes as different as hybrid zones and species fusion (4a), new speciation events, including by hybrid speciation (4b) and reinforced reproductive barriers (4c).

Fig. 4. The different mate-choice copying rules and their effects for reproductive isolation between two (or more) populations in micro-allopatry when copied preferences diverge from each other. Two copying rules apply to this scenario, promoting divergence of the copied preferences between populations. This will facilitate reproductive isolation between habitat patches.

Fig. 5. The different mate-choice copying rules and their effects for reproductive isolation between two (or more) populations in allopatry. With any of the copying rules, mate-choice copying will always promote divergent mate preferences between already isolated populations, hence facilitating new or reinforcing existent reproductive isolation between them.

Fig. 6. The different mate-choice copying rules and their effects for reproductive isolation between two (or more) populations in micro-allopatry when copied preferences agree with each other. Two copying rules apply to this scenario, promoting convergence of the copied preferences between populations. This will prevent reproductive isolation between habitat patches.

Fig. 7. The different mate-choice copying rules and their effects for reproductive isolation between two (or more) species in secondary contact. With any of the copying rules, mate-choice copying will always promote convergent mate preferences heterospecifics, hence promoting hybridization between two species previously isolated.